

A PALYNOLOGICAL STUDY OF THE GENUS *FUCHSIA* (ONAGRACEAE)¹

JOAN W. NOWICKE,² JOHN J. SKVARLA,³ PETER H. RAVEN,⁴
AND PAUL E. BERRY⁵

ABSTRACT

The pollen of 76 collections representing 48 of the ca. 100 species and all nine sections of *Fuchsia* was examined in light (LM) and scanning electron microscopy (SEM), and a selected group in transmission electron microscopy (TEM). The pollen of *Fuchsia* is shed as monads and is mostly 2-aperturate or very rarely 3-aperturate; the exine sculpture is composed of globular elements, or more rarely elongated elements; the viscin threads are segmented, more rarely smooth; the exine is composed of two layers, an outer spongy undifferentiated ectexine, and an inner solid, massive endexine. The polyploid sects. *Quelusia* (eight species) and *Kierschlegeria* (one) are characterized by 3-aperturate pollen as are several tetraploid species in sects. *Fuchsia* and *Hemsleyella*. As far as is known, 3-aperturate grains usually occur only in polyploid species; but not all polyploids have 3-aperturate pollen. Two-aperturate grains do occasionally occur in both sects. *Kierschlegeria* and *Quelusia*, where they doubtless represent the condition of the diploid ancestors. It may be concluded that the common ancestor of all extant sections of *Fuchsia* had 2-aperturate pollen, although ultimately, within the Onagraceae, the 2-aperturate condition must have been derived from 3-aperturate pollen. Most species of *Fuchsia* have a globular-type sculpture element, but sects. *Encliandra* (six species) and *Kierschlegeria* have elongated elements, a derived condition. Most species of *Fuchsia* have segmented-beaded viscin threads, but sects. *Schufia* (two species), *Jimenezia* (one) and *Kierschlegeria* (one) and some species of sect. *Encliandra* have smooth viscin threads, another derived condition. A combination of aperture number, sculpture element, and viscin thread morphology could separate the nine sections of *Fuchsia*, although palynology provides, at best, only weak evidence for distinguishing sections.

In the already highly distinctive Onagraceae, the large genus *Fuchsia* L. (100 species; Munz, 1943; Breedlove, 1969; Breedlove et al., 1982; Berry, 1982) is further distinguished by 2-aperturate pollen in most species and a berry-type fruit, two characteristics not found in any remaining taxa. Most species of this genus are shrubs and trees with red, tubular, bird-pollinated flowers, although a few have shorter flowers, not so brightly colored, yet still red or reddish in hue. Because of the distinctive flowers and berries, *Fuchsia* has traditionally been treated as a monogeneric tribe of Onagraceae. In fact, it has no obvious relationships to any other genus.

Although all the distinctive features of *Fuchsia* are clearly advanced, in overall characteristics, *Fuchsia* is one of the less specialized of the 17 genera of Onagraceae. Evidence from floral anatomy (Eyde & Morgan, 1973), wood anatomy

(Carlquist, 1975), cytology (Kurabayashi et al., 1962), and leaf architecture (Hickey, 1980) support this conclusion. The ovary of *Fuchsia* is 4-locular with a biseriate row of ovules in each. The placentation is axile but more importantly the placentas are deeply cleft, a primitive condition. *Fuchsia* is one of only three genera, *Hauya* Moc. & Sesse and *Ludwigia* L. being the other two, that lack interxylary phloem, a clearly primitive condition. Most species of *Fuchsia* are diploid, with a gametic chromosome number of $n = 11$, basic in Onagraceae. In addition, the chromosomes are relatively large for Onagraceae, lack reciprocal translocations as a regular part of the adaptive system, and are poorly differentiated into heteropycnotic and eupycnotic segments (Kurabayashi et al., 1962). In addition, Baker and Baker (1983) characterized the starchless condition found in the pollen grains of *Fuchsia* and *Lopezia* Cav. as the ancestral one, and sug-

¹ Supported in part by National Science Foundation grants to Peter H. Raven and to John J. Skvarla. We thank P. C. Hoch, J. Bittner, S. Braden, W. Chissoe, M. J. Mann, and S. Nelson for their technical assistance.

² Botany Department, Smithsonian Institution, Washington, D.C. 20560.

³ Department of Botany and Microbiology, University of Oklahoma, Norman, Oklahoma 73019.

⁴ Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.

⁵ Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 80659, Caracas 1080, Venezuela.

TABLE 1. *Fuchsia* specimens illustrated, with collector, locality to country, and Figure number(s).

Sect. <i>Ellobium</i>			
<i>Fuchsia decidua</i> Standley	Boutin 3036 (MO)	Mexico	7-9
<i>F. fulgens</i> DC.	Oliver & Voerhoek- Williams 562 (MO)	Mexico	10-12
<i>F. splendens</i> Zucc.	Burger & Stolze 5969 (MO)	Costa Rica	13-14
	Croat 515 (MO)	Costa Rica	15, 115-117
Sect. <i>Encliandra</i>			
<i>F. cylindracea</i> Lindley (<i>F. par- viflora</i> sensu Breedlove, non Lindley)	Breedlove 36037 (MO)	Mexico	67, 72
	Breedlove 15831 (DS)	Mexico	144-146
<i>F. encliandra</i> Steudel subsp. <i>encliandra</i>	Davidse & Davidse 9672 (MO)	Mexico	69
	Kalin 7089 (MO)	Mexico	59, 60
	Breedlove 15849 (DS)	Mexico	138-141
<i>F. encliandra</i> Steudel subsp. <i>tetradactyla</i> (Lindley) Breedlove	Breedlove 25920 (MO)	Mexico	135-137
<i>F. microphylla</i> H.B.K. subsp. <i>aprica</i> (Lundell) Breedlove	Breedlove 31744 (CAS)	Mexico	120-123
<i>F. microphylla</i> H.B.K. subsp. <i>hemsleyana</i> (Woodson & Siebert) Breedlove	Uteley 4297 (MO)	Costa Rica	64, 65
	Raven 20975 (DS)	Mexico	129, 130
<i>F. microphylla</i> H.B.K. subsp. <i>hidalgensis</i> (Munz) Breedlove	Breedlove 15881 (US)	Mexico	124-128
<i>F. microphylla</i> H.B.K. subsp. <i>microphylla</i>	Arizmendi 259 (MO)	Mexico	66
<i>F. microphylla</i> H.B.K. subsp. <i>quercetorum</i> Breedlove	Breedlove 22959 (CAS)	Mexico	131-134
<i>F. obconica</i> Breedlove	Breedlove 18711 (CAS)	Mexico	70, 142, 143
	Ventura 1457 (MO)	Mexico	58
<i>F. ravenii</i> Breedlove	Kalin 7090 (MO)	Mexico	61-63, 71, 118-119
<i>F. thymifolia</i> H.B.K. subsp. <i>minimiflora</i> (Hemsley) Breedlove	Breedlove 22788 (CAS)	Mexico	147-150
<i>F. thymifolia</i> H.B.K. subsp. <i>thymifolia</i>	Anderson & Laskow- ski 3993 (MO)	Mexico	57
	Pringle 9794 (MO)	Mexico	55, 56, 68
Sect. <i>Fuchsia</i>			
<i>F. ayavacensis</i> H.B.K.	Berry & Escobar 3601 (MO)	Peru	91
<i>F. boliviana</i> Carrière	Berry 3552 (MO)	Colombia	101
	Berry & Aronson 3044 (MO)	Peru	151-154
<i>F. corollata</i> Benth.	Berry 3173 (MO)	Ecuador	108
<i>F. cuatrecasasii</i> Munz	Berry 3594 (MO)	Colombia	97
<i>F. dependens</i> Hook.	Berry 3166 (MO)	Ecuador	94
<i>F. gehrigeri</i> Munz	Berry 3098 (MO)	Venezuela	90
	Berry 3296 (MO)	Venezuela	96
<i>F. hartwegii</i> Benth.	Berry 3568 (MO)	Colombia	112
	Bristol 876 (DS)	Colombia	158, 159
<i>F. hirtella</i> H.B.K.	Berry 3543 (MO)	Colombia	95
<i>F. macrophylla</i> Johnston	Berry & Aronson 3080 (MO)	Peru	103, 104

TABLE 1. Continued.

<i>F. macrostigma</i> Benth.	<i>Escobar 1094</i> (MO)	Ecuador	92, 93
<i>F. mathewsii</i> Macbride	<i>Berry 3603</i> (MO)	Peru	113
<i>F. pallescens</i> Diels	<i>Berry 3570</i> (MO)	Colombia	98
<i>F. petiolaris</i> H.B.K.	<i>Berry 3539</i> (MO)	Colombia	114
	<i>Berry 3560</i> (MO)	Colombia	99
<i>F. pringsheimii</i> Urban	<i>Tuerckheim 3151</i> (MO)	Dominican Republic	89
<i>F. putumayensis</i> Munz	<i>Berry 3562</i> (MO)	Colombia	102
<i>F. scabriuscula</i> Benth.	<i>Berry 3593</i> (MO)	Colombia	107
<i>F. tincta</i> Johnston	<i>Berry et al. 2597</i> (MO)	Peru	100, 105, 106
<i>F. triphylla</i> L.	<i>Davidse 2689</i> (MO)	Dominican Republic	88, 94
<i>F. verrucosa</i> Hartweg	<i>Berry 3286</i> (MO)	Venezuela	111, 155–157
	<i>Grant 10260</i> (US)	Colombia	109, 110
Sect. <i>Hemsleyella</i>			
<i>F. apetala</i> Ruiz & Pavón	<i>Berry & Aronson 3033</i> (MO)	Peru	74, 75, 78, 84
	<i>Berry & Aronson 3070</i> (MO)	Peru	73
<i>F. chloroloba</i> Johnston	<i>Berry et al. 2599</i> (MO)	Peru	82, 86, 87
<i>F. garleppiana</i> Kuntze & Wittm.	<i>Linderman 2030</i> (MO)	Bolivia	160–163
<i>F. inflata</i> Schulze-Menz	<i>Berry & Aronson 3012</i> (MO)	Peru	76
<i>F. juntasensis</i> Kuntze	<i>Berry 3638</i> (MO)	Bolivia	83
<i>F. membranacea</i> Hemsley	<i>Berry 3278</i> (MO)	Venezuela	85
<i>F. tillettiana</i> Munz	<i>Berry 3267-B</i> (MO)	Venezuela	79–81, 164–167
	<i>Berry 3463</i> (MO)	Venezuela	77
Sect. <i>Jimenezia</i>			
<i>F. jimenezii</i> Breedlove, Berry & Raven	<i>Allen 4965</i> (MO)	Panama	1, 2, 168, 169
	<i>Croat 36223</i> (MO)	Costa Rica	3
Sect. <i>Kierschlegeria</i>			
<i>F. lycioides</i> Andrews	<i>UC Bot. Gard. Berk. 53.1303-S2</i> (RSA) (from Hartweg in 1953)	Chile	6
	<i>Zöllner 8089</i> (MO)	Chile	4, 5, 170–173
Sect. <i>Quelusia</i>			
<i>F. bracelinae</i> Munz	<i>Mexia 4013</i> (US)	Brazil	17, 18
<i>F. campos-portoi</i> Pilger & Schulze	<i>Brade 18008</i> (S)	Brazil	19, 25
<i>F. coccinea</i> Sol.	<i>Irwin et al. 30326</i> (NY)	Brazil	31–33
<i>F. magellanica</i> Lam.	<i>Solomon & Solomon 4599</i> (MO)	Chile	20–24, 175
	<i>Raven 20560</i> (MO)	New Zealand	174
<i>F. regia</i> (Vand. ex Vell.) Munz	<i>Davidse et al. 11076</i> (MO)	Brazil	34–36
	<i>Hoehne 19661</i> (RSA)	Brazil	26–30
	<i>Ramamoorthy 680</i> (MO)	Brazil	16
Sect. <i>Schufia</i>			
<i>F. arborescens</i> Sims	<i>Feddema 2872</i> (MO)	Mexico	37–40, 191, 192
<i>F. paniculata</i> Lindley	<i>Croat 35428</i> (MO)	Costa Rica	41, 42
	<i>Allen 713</i> (MO)	Costa Rica	193, 194

TABLE 1. Continued.

Sect. <i>Skinnera</i>			
<i>F. cyrtandroides</i> Moore	van Balgooy 1785 (MO)	Tahiti	46, 49, 50, 181-185
<i>F. excorticata</i> (J. R. Forster & G. Forster) L. f.	McMillan 65/91 (MO)	New Zealand	43, 44, 51, 54, 178, 180
	Carse 2312 (MO)	New Zealand	176, 177, 179
<i>F. perscandens</i> Cockayne & Allen	Raven et al. 25212 (MO)	New Zealand	45, 53, 186, 187
<i>F. procumbens</i> Cunn.	Walker 4730 (MO)	New Zealand	47, 48, 52
	Cultivated Univ. of California Botanical Garden, Berkeley UCB 49.812 (UC)	New Zealand	188-190

gest that the starchy condition found in all remaining genera may be derived. The geographical distribution of *Fuchsia* could also be cited as evidence of its relative primitive position within the subfamily, since it clearly centers in South America (where the family almost certainly originated; Raven & Axelrod, 1974; Raven, 1979), with others in New Zealand-Tahiti and in Central America-Mexico.

Fuchsia is modally outcrossing, largely because of a combination of protogyny and spatial separation of anthers and stigma (Raven, 1979; Berry, 1982). In addition, male-sterility occurs in the sects. *Encliandra*, *Kierschlegeria*, *Schufia*, and *Skinnera*, and, together with female-sterility in most of the same species enforces outcrossing by dioecism, subdioecism, or, in two species of sect. *Skinnera*, by gynodioecism.

Advanced features in *Fuchsia* include those associated with bird pollination—red, tubular flowers—and bird dispersal of seeds—berries. These features make it very unlikely that plants with the characteristics of *Fuchsia* could have evolved before the Eocene (Raven, 1979; Sussman & Raven, 1978), whereas the known fossil record of the family extends back to the uppermost Cretaceous (Eyde & Morgan, 1973). The 2-aperturate pollen of most species of *Fuchsia* is unique in Onagraceae and nearly so in all of the Myrtales, and is a clearly derived feature. The nine sections of *Fuchsia* may be summarized as follows:

Sect. *Ellobium* consists of three species in Mexico and Central America formerly assigned to sects. *Fuchsia* and *Hemsleyella* (Breedlove et al., 1982). Sect. *Ellobium* combines character-

istics of each of these basically South American sections, having petals as in sect. *Fuchsia* and band-nectaries as in sect. *Hemsleyella*. Sect. *Ellobium* may represent a Neogene invasion of Central America-Mexico by the same stock that gave rise to these sections.

Sects. *Encliandra* (Breedlove, 1969), *Jimenezia*, and *Schufia* have seven, one, and two species respectively, and occur in Mexico and Central America. The presence of small flowers, lobed-adnate nectaries, and smooth viscin threads suggest a common ancestry (Berry, 1982), as does the geographical proximity of these sections. All nine species are diploid, with $n = 11$ (Breedlove, 1969; Breedlove et al., 1982). Sect. *Schufia* can be easily distinguished from all other species of *Fuchsia* by the large, many-flowered, terminal panicles in which the small flowers have stamens exerted beyond the floral tube. These three sections apparently represent an earlier invasion of Central and North America than that which gave rise to sect. *Ellobium*.

Sect. *Fuchsia* includes 61 species, 59 from the tropical Andes of South America, and the other two in Hispaniola (Berry, 1982). This is the only section with annular nectaries in all but three species. The flowers have petals, in contrast to those of the sympatric sect. *Hemsleyella*, and the floral tubes are longer than the sepals, *F. verrucosa* excepted. Of the 43 species in sect. *Fuchsia* for which chromosome numbers have been reported, 37 were diploid with $n = 11$, five were tetraploid with $n = 22$, and one included both diploid and tetraploid individuals.

Sect. *Hemsleyella*, the second largest with 14 species, is found in the tropical Andes, as is sect.

Fuchsia. It differs from the latter by the absence of petals and its adaptations to a largely epiphytic habitat: tuberous stems and dry-season flowering and leaf drop (Berry, 1982). In fact, most herbarium specimens of sect. *Hemsleyella* lack leaves. Some species are polyploid (Berry, unpubl. data).

Sect. *Kierschlegeria* has a single species, the only one in the genus to occur in a seasonally dry habitat (Berry, 1982). *Fuchsia lycioides* has small deciduous leaves, spinose leaf bases, and thick seed coats, characteristics associated with xerophytic conditions. The flowers are small and solitary in the axils of leaves on (mostly) unbranched, peculiarly straight stems. It is subdioecious (Atstatt & Rundle, 1982). Like sect. *Quelusia*, it is tetraploid and has 3-aperturate pollen.

Sect. *Quelusia* exhibits a common pattern of disjunct distribution, seven species in southeast coastal Brazil, and an eighth, the widely cultivated *F. magellanica*, in the southern half of Chile and eastward into the western slopes of the Andes in Argentina. All species are polyploid and all have 3-aperturate pollen.

The four species of sect. *Skinnera* are the only representatives of the genus that occur in the Old World, three in New Zealand and one in Tahiti. These species are characterized by reduced petals, band-type nectaries, and the smallest and most numerous seeds in the genus. It seems likely that sect. *Skinnera* separated in Paleogene time from the ancestral stock, as judged from fossil evidence and the time needed to produce the present diversity in habit among the three New Zealand species, one a creeper, the second a liana, and the third a tall forest tree (see discussion in Berry, 1982).

This paper is intended to be a companion report to Praglowski et al. (1983), which comprises a survey of *Fuchsia* and *Ludwigia* pollen using predominantly light microscopy.

MATERIALS AND METHODS

Anthers were removed from herbarium specimens, all material for LM and SEM was acetolyzed according to procedures outlined in Erdtman (1966). Samples for SEM were either sputter or vacuum coated with gold and examined with an ISI Super II, a Cambridge Stereoscan MK IIa and S410, or a Coates and Welter 106B Field Emission Microscope.

The species examined, collection data, and fig-

ure number(s) are given in Table 1. Most of the collections used in this study were also reported in Praglowski et al. (1983), and there are presented both illustrations and extensive pollen morphological data on all collections. Although virtually all of the collections cited in the earlier study were examined for this report, not all specimens are illustrated here, either because of closely similar morphology (especially in sect. *Fuchsia*) or because they were illustrated already in Praglowski et al. (1983).

For TEM, pollen samples were acetolyzed or rehydrated (unacetolyzed). In the former, the residue was incorporated into agar, dehydrated through a graded acetone series and embedded in Araldite-Epon resins. Prior to incorporation in agar, the pollen was stained in 1–2% OsO₄ buffered with sodium cacodylate at pH 7.2–7.4 for 1–2 hours at room temperature. Unacetolyzed pollen was rehydrated by Alcian blue (Rowley & Nilsson, 1972) or by softening in Vatsol (Pohl, 1965), soaking for 2–3 days in 2.5% sodium cacodylate buffered (pH 7.2) glutaraldehyde. Dehydration and embedding follows that described above, except that agar was not used.

Sections approximately 10 nm thick were cut with diamond knives, collected on uncoated copper grids, and stained for 5 minutes each in 0.5% aqueous uranyl acetate and lead citrate, or in rehydrated pollen only in lead citrate. Observations and electron micrographs were made with either a Philips model 200 or Zeiss 10 electron microscope at 40 kV.

The terms for sculpture elements that are used in the palynological description of *Fuchsia* in this paper are documented elsewhere (Praglowski et al., 1983).

Light slides of all samples are deposited at the Palynological Laboratory, Department of Botany, Smithsonian Institution.

RESULTS

Mature pollen of *Fuchsia* is shed as monads, is paraisopolar to heteropolar, 2-aperturate and bilaterally symmetrical (Figs. 1, 7, 10, 13, 37, 40, 41, 43–48, 55, 58–61, 64, 73, 74, 79, 82–86, 88–92, 103–107, 109, 112–114), or, more rarely, 3-aperturate and radially symmetrical (Figs. 4, 16–21, 33–36, 76, 108, 180, 181).

SHAPE

The shape in polar view is \pm elliptic in 2-aperturate grains (e.g., Figs. 1, 10, 40, 59, 89, 92, 109, 114), or triangular in 3-aperturate grains

(e.g., Figs. 4, 17, 19, 20, 36, 76, 108). The shape in aperture-centered equatorial view is \pm ovoid in 2-aperturate grains (Figs. 85, 86, 103, 105), or apiculate in 3-aperturate grains (Figs. 18, 21). The shape in mesocolpus-centered equatorial view is \pm apiculate in both 2- and 3-aperturate grains (Figs. 34 uppermost grain, 43, 55, 58, 84, 104, 106).

APERTURES

The apertures protrude and are formed by a cone-like extension of the exine (Figs. 35, 93, 122, 128, 132, 136, 143, 155, 171, 176, 177, 191, 193). The endoaperture is complex and consists of a massive deposition of endexine in the form of ring(s). The chamber-like area delimited by the endoapertural ring proximally and by the ectoaperture (see below) distally, has been designated as the vestibulum (Pragłowski et al., 1983). At the base of the cone and partially extending into the body of the grain the endexine is coarsely granular; within the vestibulum it is also finely channeled (Figs. 119, 122, 128, 132, 136, 143, 155, 163, 171, 174, 176, 177, 188, 191, 193). The ectoaperture is irregular in shape (Figs. 38, 51, 85, 86, 103, 105), only rarely a well-defined pore (Figs. 28, 93) or a horizontally-oriented colpus. Rare 4-aperturate grains were observed (Fig. 32) in the 3-aperturate sect. *Quelusia*, and 3-aperturate grains were noteworthy in *F. inflata* (sect. *Hemsleyella*), and *F. procumbens*, *F. excorticata* (Fig. 180), and *F. cyrtandroides* (Fig. 181) of sect. *Skinnera*, which is characterized by 2-aperturate pollen.

EXINE

The exine is distinctly bizonal (cf. many examples illustrated in Figs. 115–194), composed of ektexine and endexine. The ektexine consists of an outer spongy or paracrystalline-beaded layer without organization into distinct tectum, columellae, and foot layer components. The endexine is the mostly solid and continuous layer. The inner surface is finely granular in the body of the grain and very coarsely granular and/or lamellate within the apertures (see numerous examples in Figs. 115–194). The two exine layers are closely associated with one frequently appearing to extend into the other (e.g., Figs. 121, 124, 125, 130, 133–135, 138, 142, 149, 150, 160, 161, 168–170, 172, 178, 179, 183, 186, 189, 192, 194).

Sculpturing of the ektexine consists of elements which are primarily globular or irregular

spheres (Figs. 2, 3, 14, 15, 27, 30, 53, 54, 57, 95, 98–102, 126, 147, 182), or elongated units (Figs. 5, 6, 56, 63, 66, 70–72, 129). Sometimes the elements were transitional and therefore difficult to categorize (i.e., Fig. 144).

VISCIN THREADS

Viscin threads are extensions of the ektexine (Figs. 126, 130, 138, 141, 142, 144, 145, 147, 152, 153, 158–161, 164, 172, 178, 179, 182, 183, 186, 190, 192). While they are usually located near or about the central region of the proximal face (Figs. 1, 10, 17, 59, 73, 88, 89, 92, 109, 112, 114, 181), they have also been noted to or on, the apertural protrusion (Figs. 141, 145, 188, 190). In freshly collected or rehydrated pollen, the viscin threads are enclosed by a membrane (Figs. 117, 152–154, 164–167, 172, 173, 178, 192). Threads are mostly segmented-beaded (Figs. 9, 12, 14, 15, 22–27, 52–54, 75, 87, 94–97, 101, 102, 117, 153, 154, 158–161, 165–167, 178, 182–187, 190) to segmented-ropy (Figs. 57, 98–100, 126, 147), or less commonly smooth (Figs. 2, 3, 5, 6, 31, 39, 42, 49, 50, 62, 63, 65, 66, 69–72, 110, 111, 123, 130, 131, 138–141, 144, 145, 157, 173).

In some species it is difficult to recognize the morphological pattern and the threads consist of both smooth and segmented portions (see, for example, *F. ravenii*, Fig. 71). Light segmentation (e.g., *F. cyrtandroides*, Figs. 49, 50, 182, 185; *F. perscandens*, Fig. 187) characterizes some species and usually requires supporting evidence from transmission electron microscopy (Figs. 183, 184, 186).

Localized distensions also contribute to thread morphology. One type, illustrated by *F. cyrtandroides* (Fig. 50) and *F. verrucosa* (Fig. 111) shows inflated bases and results from several threads originating from the exine surface within a confined area. This is common throughout Onagraceae, most notably in *Epilobium* (Skvarla et al., 1978). Another type is that of nodular distensions along the threads (e.g., *F. coccinea*, Fig. 31; *F. cyrtandroides*, Fig. 49), which probably represents a "rolling up" of certain thread regions. Threads characterized by nodular or "ball-like" distensions are usually associated with the more complex compound threads of *Epilobium* and *Boisduvalia*. The last type of distension occurs on smooth threads and appears cylindrical. This is observed on most smooth threads throughout the family (Skvarla et al., 1978).

TABLE 2. Pollen morphology in *Fuchsia*.

Sections	Number of Species in Section	Pollen Apertures	Predominant Ektexine Sculpture	Viscin Threads ^a
<i>Ellobium</i>	3	2	globular-type	segmented-beaded
<i>Encliandra</i>	7	2	elongated	smooth, sparsely segmented (segmented-ropy)
<i>Fuchsia</i>	61	2 (3)	globular-type ^b	segmented-beaded ^c
<i>Hemsleyella</i>	14	2 (3)	globular-type	segmented-beaded
<i>Jimenezia</i>	1	2	globular-type	smooth
<i>Kierschlegeria</i>	1	3	elongated	smooth
<i>Quelusia</i>	8	3	globular-type	segmented-beaded
<i>Schufia</i>	2	2	globular-type	smooth
<i>Skinnera</i>	4	2 (3)	globular type	segmented-beaded

^a Term for viscin thread morphology follows Skvarla et al. (1978).

^b Elongated in *F. verrucosa*.

^c Smooth in *F. verrucosa*.

The pollen morphology of the sections of *Fuchsia* is characterized briefly as follows, and summarized in Table 2:

Sect. *Ellobium* (Lilja) Breedlove, Berry & Raven. Figures 7–15, 115–117.

Three species, Mexico and Central America.

Pollen was similar, 2-aperturate with a globular type ektexine sculpture and segmented-beaded viscin threads.

Sect. *Encliandra* (Zucc.) Endl. Figures 55–72, 118–150.

Seven species, Mexico and Central America.

Pollen of sect. *Encliandra* was predominantly 2-aperturate with an elongated type of ektexine sculpture. Viscin threads in this section were primarily smooth (Figs. 65, 66, 69, 71, 144), although sparsely segmented (Figs. 62, 63, 67, 68, 70–72), and segmented-ropy (Figs. 57, 147) threads were also common.

Sect. *Fuchsia*. Figures 88–114, 151–161.

Sixty-one species, tropical Andes and Hispaniola.

Almost all species examined in sect. *Fuchsia* had similar pollen: 2-aperturate (Figs. 88–92, 103–107, 109, 112–114) with globular type ektexine sculpture and segmented-beaded viscin threads, two characteristics illustrated best at high magnification ($\times 15,000$), Figures 100–102. One collection of *Fuchsia corollata*, Berry 3173, had predominantly 3-aperturate grains.

The type species for this section and thus for the genus is *F. triphylla* (Figs. 88, 94) endemic to Hispaniola, as is one other species *F. pringsheimii* (Fig. 89). Both are tetraploid, but have

2-aperturate grains (for discussion, see Berry, 1982: 37).

Fuchsia verrucosa (Figs. 109–111) differed in thread type and ektexine sculpture. The threads were smooth and usually originated from a “whorled base,” and the sculpture element in the Colombian collection is elongated (Fig. 110), and more irregularly-shaped in the Venezuelan collection (Fig. 111). Berry (1982) considered this species one of the most distinctive in the section on the basis of its short floral tubes, antesealous nectary lobes, and tetraploidy with 2-aperturate pollen grains.

Sect. *Hemsleyella* Munz. Figures 73–87, 162–167.

Fourteen species, tropical Andes of South America.

Pollen of all species of sect. *Hemsleyella* was similar: predominantly 2-aperturate, segmented-beaded viscin threads and with a globular type sculpture element. In one collection of *F. inflata*, Berry & Aronson 3012 (Fig. 76), approximately three-fourths of the grains were 3-aperturate. An equatorial ridge appeared particularly pronounced in some species of sect. *Hemsleyella*, e.g., *F. tillettiana*, Figure 79 (see Praglowski et al., 1983: 5).

Sect. *Jimenezia* Breedlove, Berry & Raven. Figures 1–3, 168, 169.

One species, Costa Rica and Panama.

Pollen of *F. jimenezii* was 2-aperturate with a globular type sculpture and smooth viscin threads that can be single or compound. In this species the viscin threads originated over a wide area of the proximal surface.

Sect. *Kierschlegeria* (Spach) Munz. Figures 4–6, 170–173.

One species, coastal Chile.

Pollen of *F. lycioides*, a tetraploid species, was 3-aperturate with an ektexine that had an elongated element sculpture and smooth viscin threads.

Sect. *Quelusia* (Vand.) DC. Figures 16–36, 174, 175.

Eight species, SE coastal Brazil, Chile, and Argentina.

Pollen of sect. *Quelusia* was 3-aperturate (Figs. 16, 17, 33–36) with a globular type of ektexine sculpture. Rare 4-aperturate grains were noted (Fig. 32). The viscin threads were segmented-beaded (Figs. 22–27, 29, 30). In *F. coccinea* (Fig. 31) the threads were only slightly segmented and had nodular distensions (see also *F. cyrtandroides*, Fig. 49). All species of this section are polyploid.

Sect. *Schufia* (Spach) Munz. Figures 37–42, 191–194.

Two species, Mexico to Panama.

Pollen of the closely related *F. arborescens* and *F. paniculata* was similar: 2-aperturate with a globular type ektexine sculpture and smooth viscin threads.

Sect. *Skinnera* (Forster) DC. Figures 43–54, 176–190.

Four species, three in New Zealand and one in Tahiti.

The pollen of sect. *Skinnera* was 2-aperturate (a few 3-aperturate grains in *F. cyrtandroides*, Fig. 181; *F. excorticata*, Fig. 180; and *F. procumbens*) with a mostly globular type ektexine sculpture (slightly elongate in *F. cyrtandroides*, Fig. 50). A trend in viscin thread segmentation was evident: prominent segmented-beaded threads in *F. excorticata* (Figs. 54, 163, 164) and *F. procumbens* (Figs. 52, 190), less prominent segments in *F. perscandens* (Figs. 53, 186, 187), and light segmentation in *F. cyrtandroides* (Figs. 49, 50, 182–185). At low-intermediate SEM magnifications (Figs. 49, 50) segmentation in *F. cyrtandroides* was not clearly evident and thread morphology appeared smooth (see Praglowski et al., 1983: 21). At higher SEM magnification light segmentation was evident in the threads (Figs. 182, 185). These segments were better defined with TEM (Figs. 183, 184).

DISCUSSION

The most conspicuous variation in the pollen of *Fuchsia* is that of aperture number, which also

determines shape of the grain and the type of symmetry. Most of the species in the largest section, sect. *Fuchsia* (Figs. 88–92, 103–107, 109, 112–114) have predominantly 2-aperturate grains, as do the species of sects. *Jimenezia* (Fig. 1), *Ellobium* (Figs. 7, 10, 13), *Schufia* (Figs. 37, 40, 41), *Skinnera* (Figs. 43–48), *Encliandra* (Figs. 55, 58–61, 64), and *Hemsleyella* (Figs. 73, 74, 79, 82–86). The entirely polyploid sects. *Quelusia* (Figs. 16–21, 32–36) and *Kierschlegeria* (Fig. 4) are characterized by 3-aperturate grains as are several polyploid species in sects. *Fuchsia* and *Hemsleyella*. In one collection of *F. inflata* (sect. *Hemsleyella*), *Berry & Aronson 3012*, the majority of the grains were 3-aperturate (Fig. 76). In many other plants the number of apertures in the pollen is affected by level of polyploidy. Our data (for the entire family) support this contention: deviations from the standard 3-aperturate conditions—i.e., four or five—are found in polyploids. Warth (1925) reported that a single tetraploid individual of sect. *Encliandra* had about 50% 3-aperturate pollen in contrast to the consistently diploid and 2-aperturate condition of other plants in this section. Similarly, Berry (1982: 37) has reported high proportions of 3-aperturate pollen in two of the six wholly or partly tetraploid taxa of sect. *Fuchsia*.

The wide distribution of 2-aperturate pollen in diverse sections of *Fuchsia*, including the very distinctive and only Old World section, sect. *Skinnera*, would favor the hypothesis that the 3-aperturate condition of a few species in the genus is directly associated with polyploidy and derived wherever it occurs.

In *F. lycioides* (sect. *Kierschlegeria*), about 25% of the grains examined by Praglowski et al. (1983) were 2-aperturate, as were occasional grains of one sample of *F. magellanica* (sect. *Quelusia*). Most likely these examples represent reversions to the ancestral condition of the diploids from which the tetraploids were derived, rather than separate origins of a character that is otherwise unknown in the family. We may conclude that the common ancestor of all extant species of *Fuchsia* had 2-aperturate pollen.

The predominant exine sculpture in *Fuchsia* and in most Onagraceae consists of globular type elements, which have varying degrees of distinction, e.g., in Figures 2 and 3 (*F. jimenezii*) the elements protrude, some even appear to be discrete spheres, whereas in Figures 27 (*F. regia*) and 77 (*F. tillettiana*) the elements appear more “submerged.” This condition, globular-type elements, is probably primitive for the genus. The

second sculpture type consists of elongated elements and is illustrated best in Figures 5 (*F. lycioides*), 65 (*F. microphylla* subsp. *hemsleyella*), and 70 (*F. obconica*). In general, the six species of the advanced sect. *Encliandra* and the only species in sect. *Kierschlegeria* mainly have elongated exine elements.

Judging from the data presented in this paper, as well as that of Skvarla et al. (1978), the viscin threads of *Fuchsia* are among the most copious in Onagraceae (Figs. 29, 75, 77, 78, 86, 96, 106, 112) and their interpretation as extensions of the ektexine (Skvarla et al., 1978) is strikingly illustrated (e.g., Figs. 130, 138, 141, 142, 145, 152, 153, 158–161, 178, 179, 186, 190, 192). These threads hold large masses of pollen together, presumably for more efficient pollination. The copious aspect of *Fuchsia* threads may be associated with bird pollination. The fact that these threads maintain the pollen in masses even after acetolysis would substantiate their effectiveness in nature. As pointed out by Raven (1979), sparse development of viscin threads is associated with pollination by bees, which are actually concerned with gathering pollen as food.

As shown in Table 2, segmented viscin threads are characteristic of most species of *Fuchsia*, and this is clearly the primitive condition in the genus. Smooth viscin threads of the derived and presumably directly related sects. *Encliandra*, *Jimenezia*, and *Schufia*, as well as those of the unrelated but still clearly derived sect. *Kierschlegeria*, clearly represent an advanced condition in these groups. There is a considerable amount of variability in viscin thread morphology in *Fuchsia microphylla* (sect. *Encliandra*): one subspecies, *F. microphylla* subsp. *hidalgensis* (Fig. 126), had segmented-ropy viscin threads; while others, subsp. *aprica* (Fig. 123), *hemsleyana* (Figs. 64, 130), *microphylla* (Fig. 66), and *quercetorum* (Fig. 131), had smooth threads.

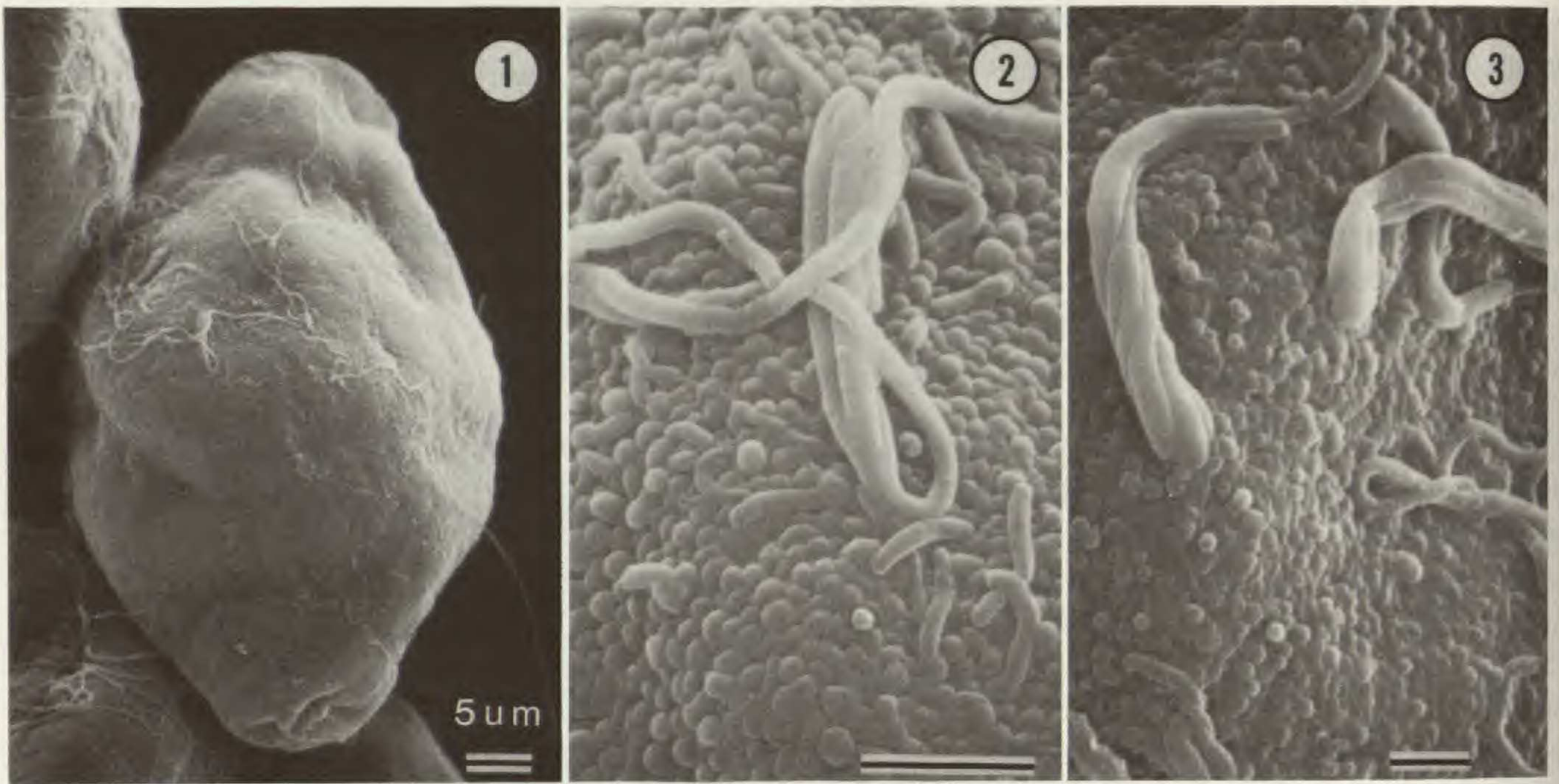
In a recently published paper, Hesse (1982) described the development of viscin threads in *Epilobium angustifolium* and an unnamed species of *Fuchsia*. According to him, viscin threads develop in a granular matrix, and then the threads "approach towards" the microspores and "tend to fuse with the ektexine." In all Onagraceae the viscin threads are attached on the proximal face near the pole. In the case of pollen that is shed as tetrads, it is difficult for us to visualize a migration of threads between closely associated tetrad members, and their subsequent attachment to the pole.

The structure of the exine in *Fuchsia* and in

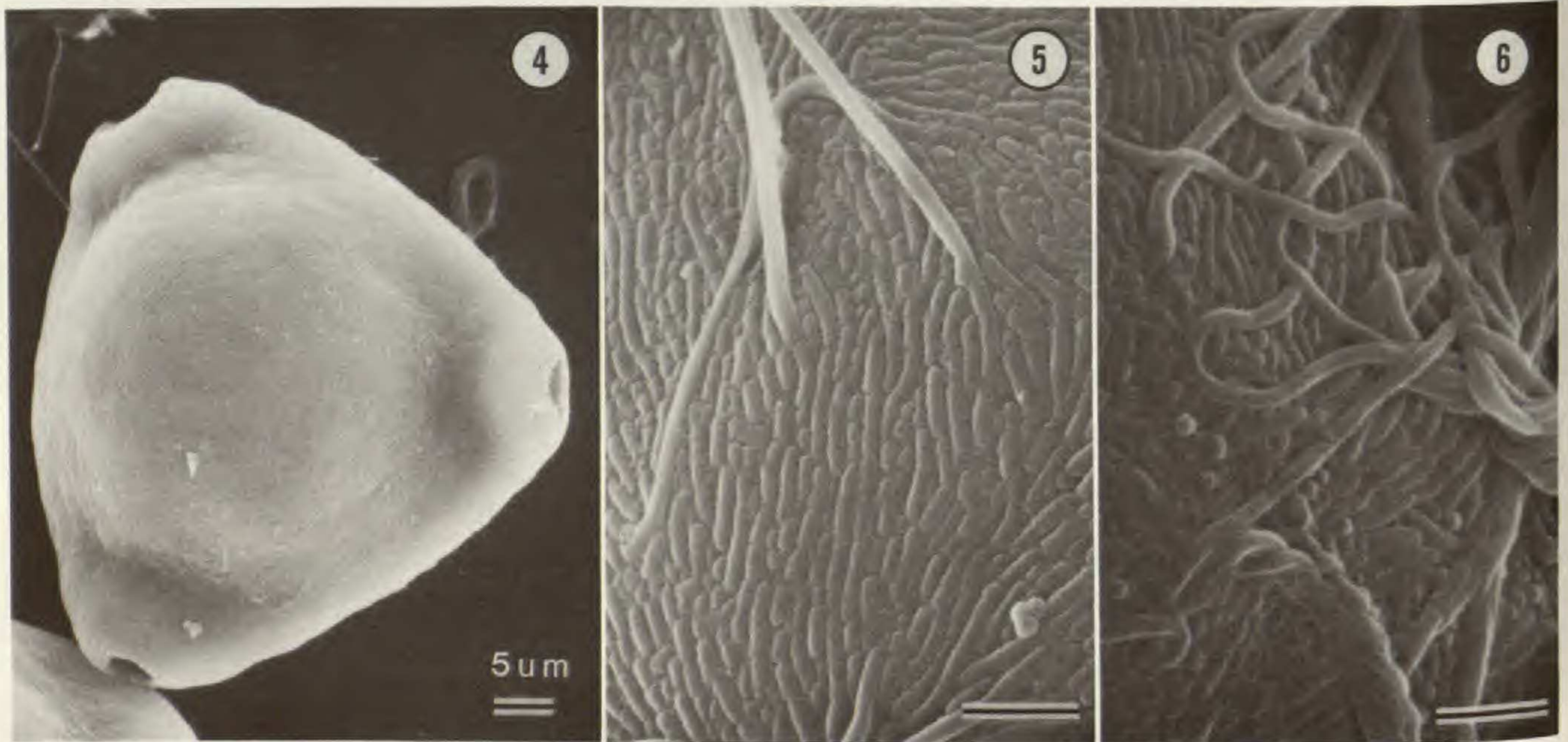
most other Onagraceae (Skvarla et al., 1976) is unique within the angiosperms (Patel et al., 1984). The ektexine is not differentiated into tectum, columellae, and foot layer units; instead, it consists of a spongy or paracrystalline layer, which is united with the endexine at numerous points along the ektexine-endexine interface. This selected union (rather than a total union or blanketing which would be expected in columellaless pollen) can result in a misleading impression that vestigial or incipient columellae are present. These structural relationships are clearly evident by perusal of many of the TEMs in Figures 115–194 as well as in SEM of fractured pollen (see particularly Figs. 120, 129). The ektexine is relatively uniform within a grain, differing sometimes in thickness between the distal and proximal faces (Pragłowski et al., 1983; e.g., Figures 115, 116, 124, 125, 145, 146, 189, 190), and in the degree of fusion of the spongy elements. Organization of the spongy-paracrystalline ektexine suggests that some ektexines are more "complete" than others. For example, the ektexine in *F. microphylla* subsp. *hidalgensis* (Figs. 124, 125) seems to have more fused elements, hence more ektexine area than *F. garleppiana* (Fig. 162). Although this has certain validity, examination of the included TEMs (Figs. 115–194) will show that "completeness" or "incompleteness" of the ektexine will vary within the nine sections of *Fuchsia* and possibly even within species (compare TEM of subspecies of *F. microphylla*, Figs. 121, 122, 124, 125, 128, 130, 132–134). The second exine layer, the endexine, is primarily massive and uniform. As mentioned elsewhere, the lower or inner margin is usually finely granular throughout the pollen grain body, while in the aperture protrusions the endexine is extraordinarily channeled as well as being coarsely granular.

These results agree with previous work which considered the ektexine pattern of *Fuchsia* as having "tectum and columellae virtually indistinguishable" (Skvarla et al., 1976: 452). In this earlier study the ektexine pattern of *F. microphylla* subsp. *quercetorum* was described and illustrated (p. 51 and pl. 1F) as having "tectum and columellae distinct." Reexamination of this taxon clearly shows that the "columellae" were enhanced because the sectional view was exactly at the junction of the exine and cone-like aperture protrusion. Therefore, it is now more appropriate to recognize this exine layer simply as ektexine.

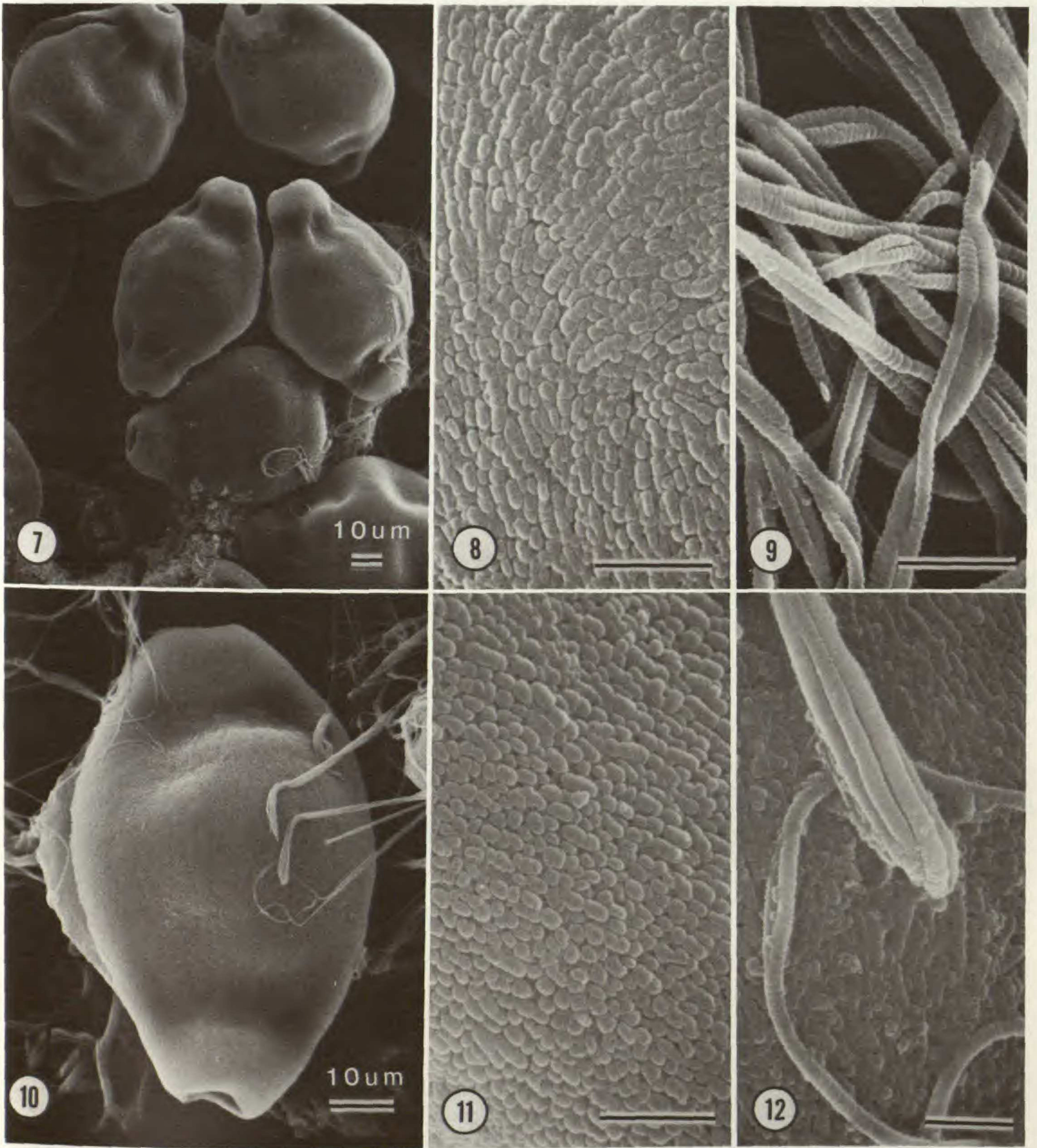
In the pollen of *Fuchsia*, two characteristics



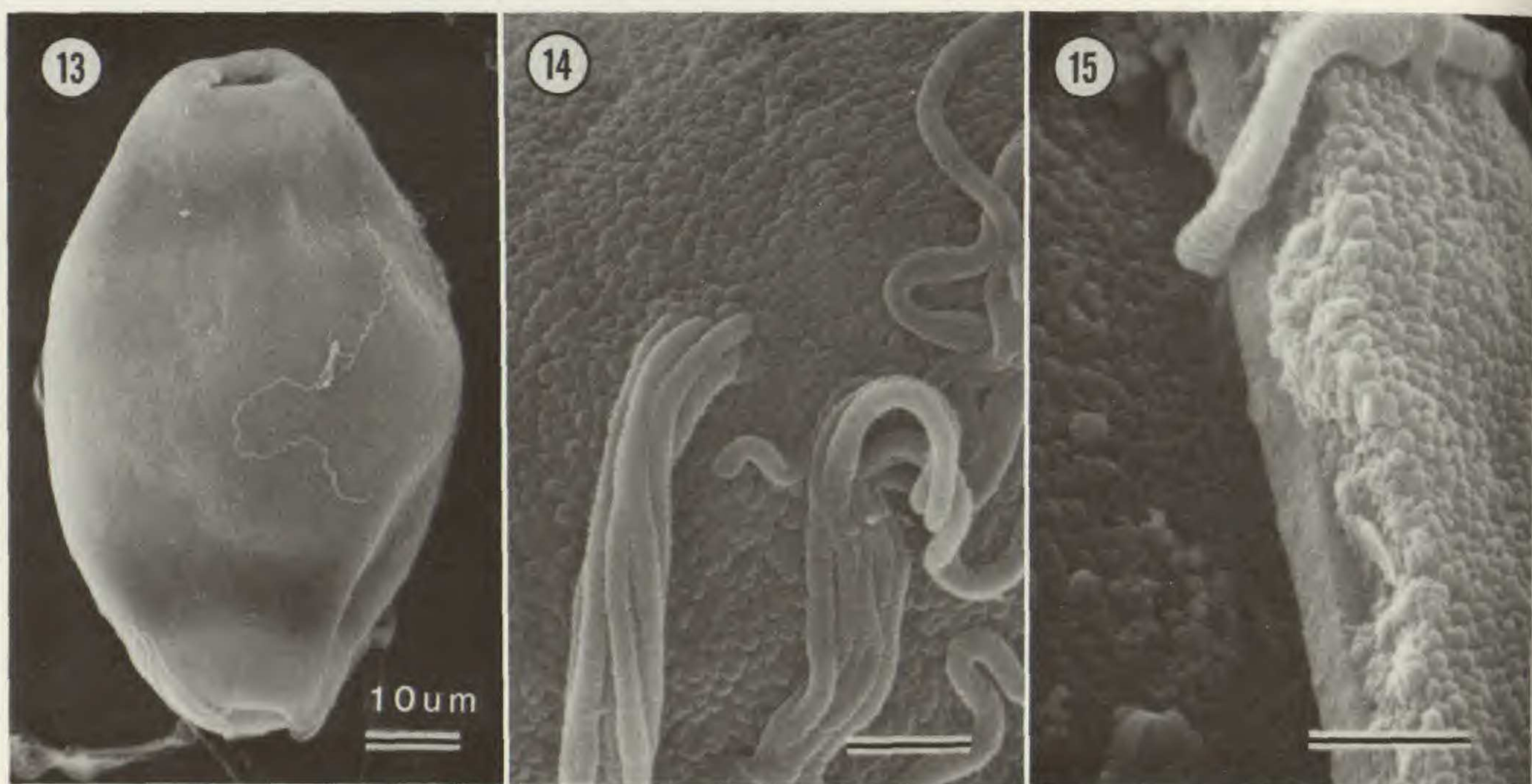
FIGURES 1-3. Scanning electron micrographs of *Fuchsia* sect. *Jimenezia*, *F. jimenezii*.—1. Slightly oblique polar view.—2. Ektexine with globular element sculpture and smooth viscin threads.—3. See legend of Figure 2. The scale equals $2\ \mu\text{m}$, unless otherwise indicated.



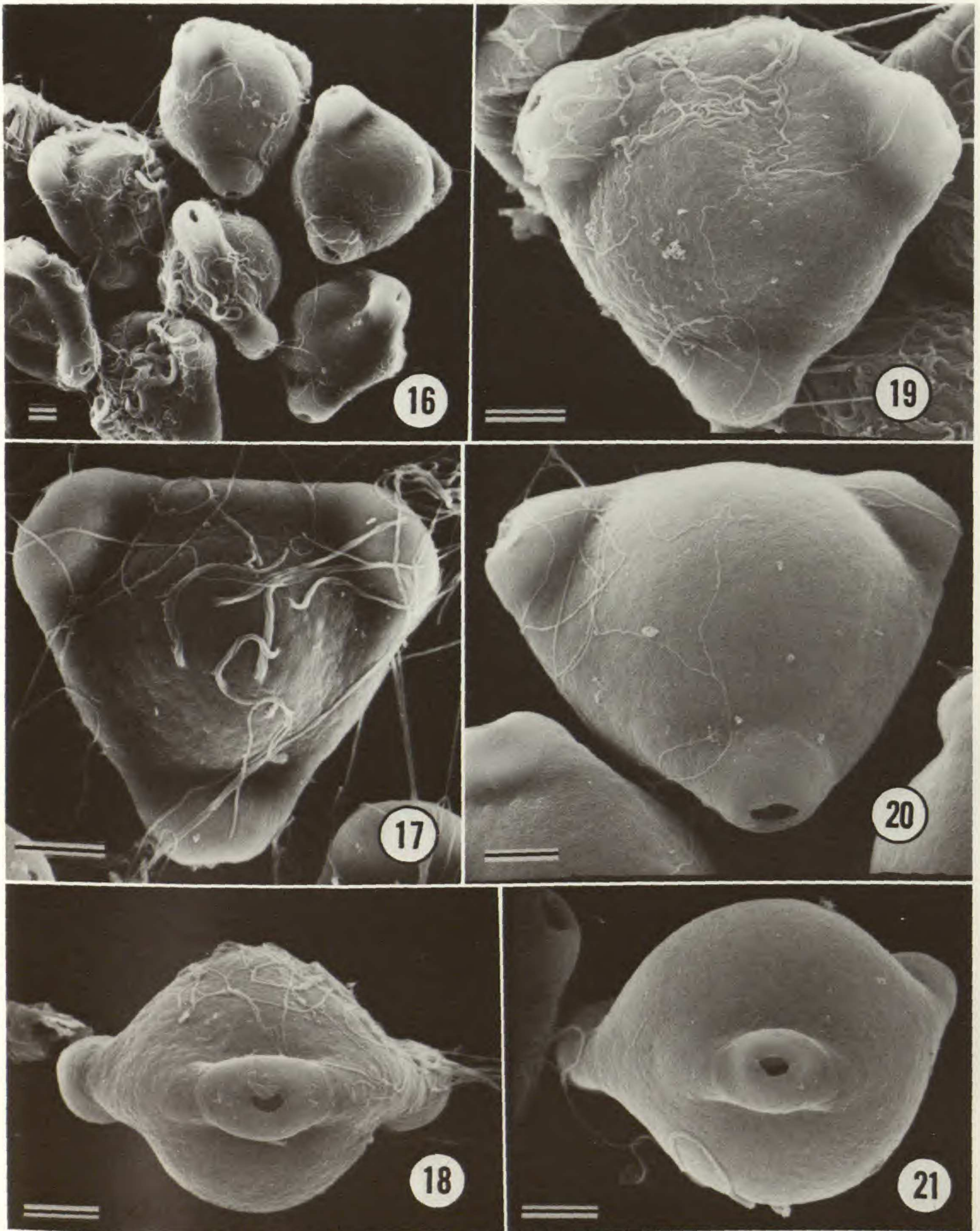
FIGURES 4-6. Scanning electron micrographs of *Fuchsia* sect. *Kierschlegeria*, *F. lycioides*.—4. Distal polar view.—5. Ektexine with elongated element sculpture and smooth viscin threads.—6. See legend of Figure 5. The scale equals $2\ \mu\text{m}$, unless indicated.



FIGURES 7-12. Scanning electron micrographs of *Fuchsia* sect. *Ellobium*. 7-9. *F. decidua*.—7. Low magnification of group.—8. Ektexine with globular-elongated element sculpture.—9. Segmented viscin threads. 10-12. *F. fulgens*.—10. Proximal polar view illustrating thread attachment.—11. See legend of Figure 8.—12. Segmented viscin threads. The scale equals 2 μm , unless indicated.

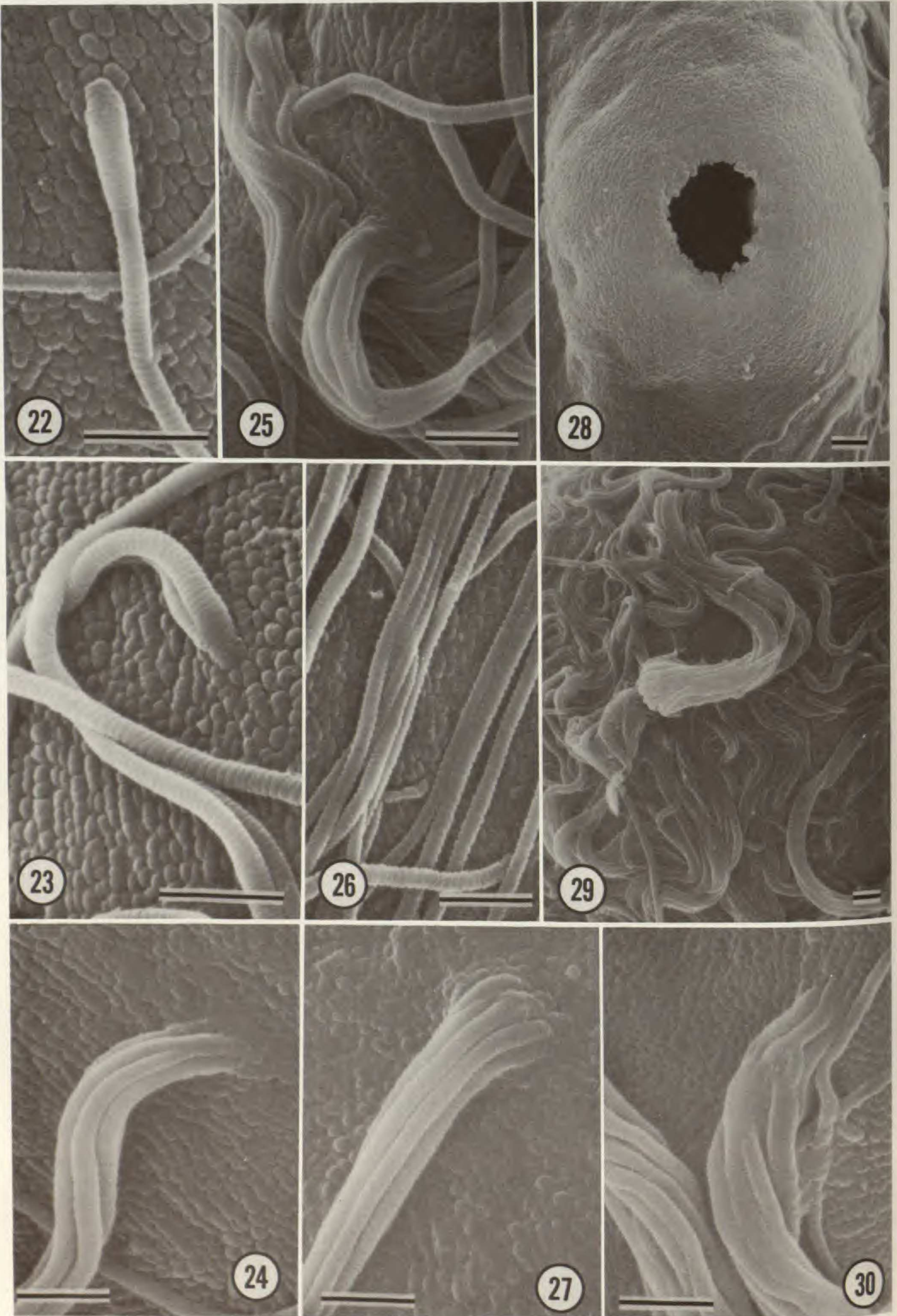


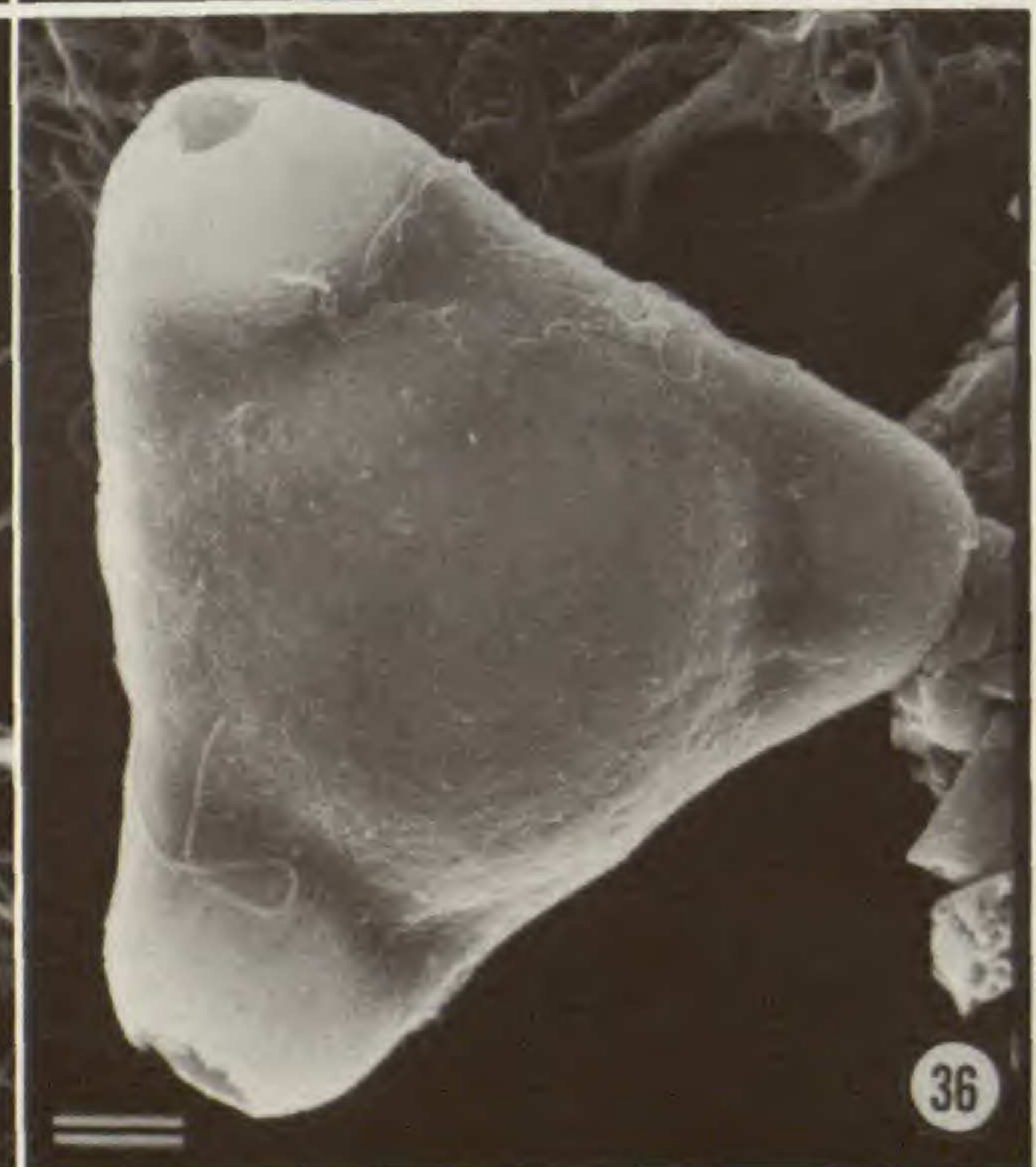
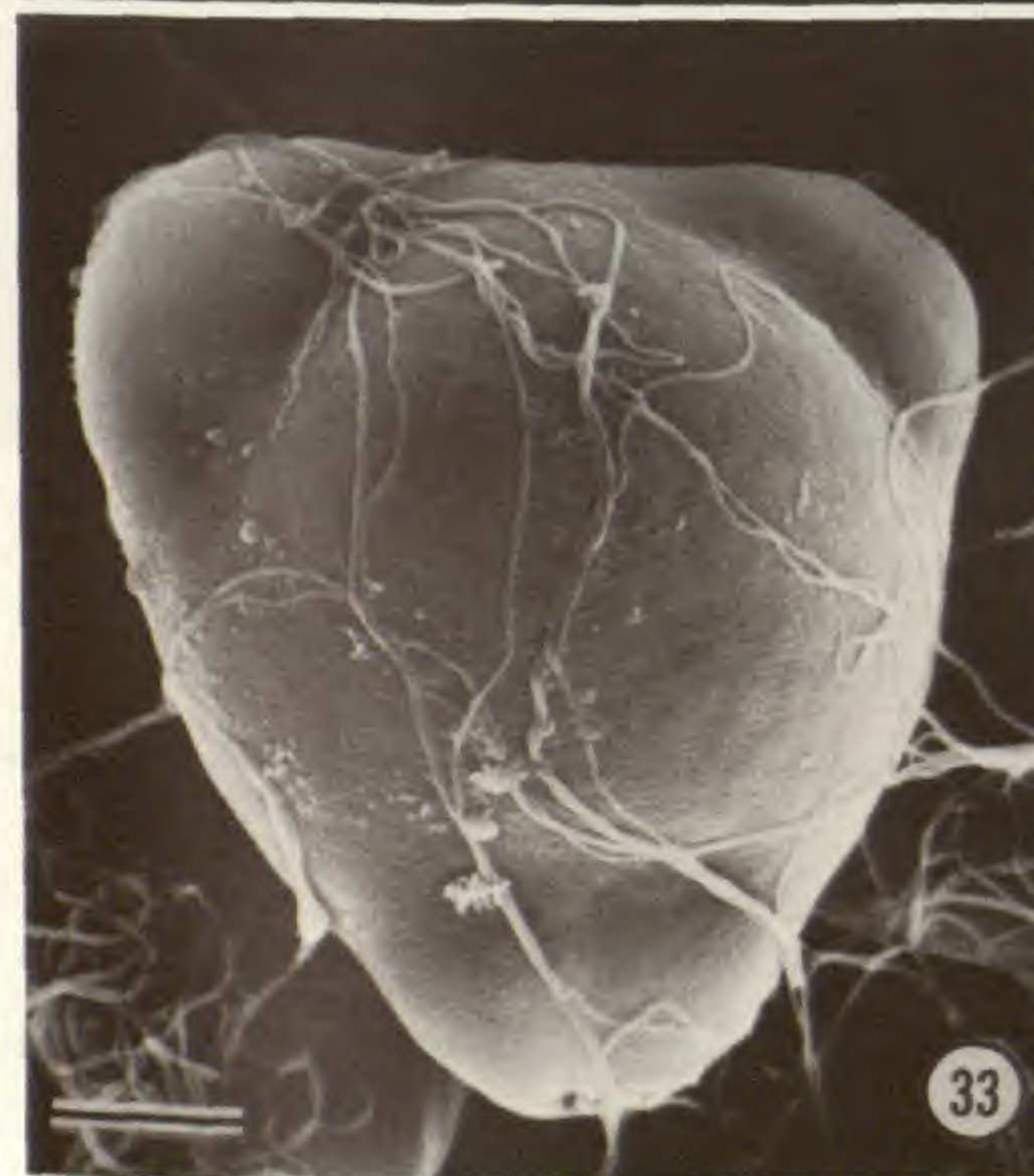
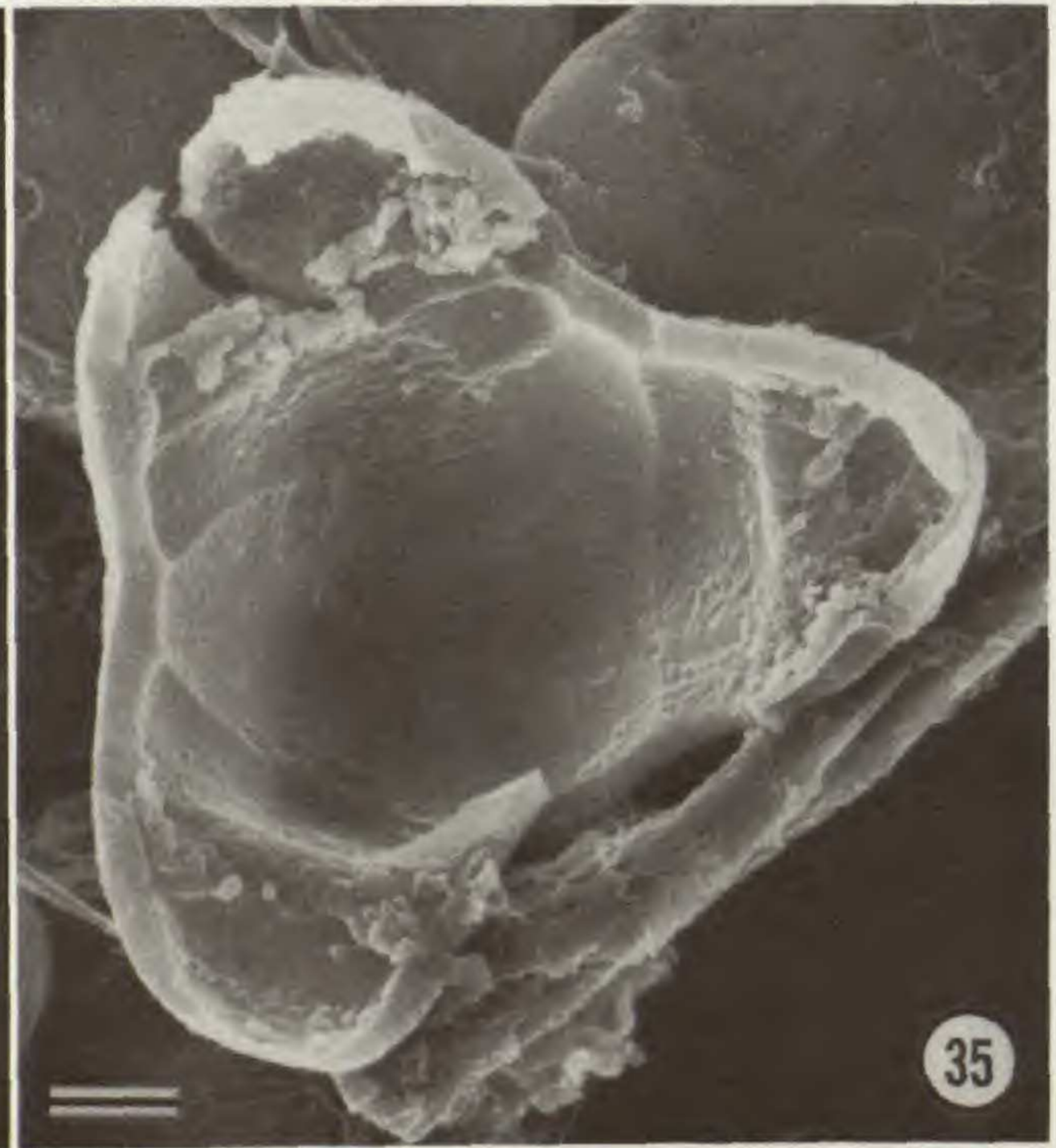
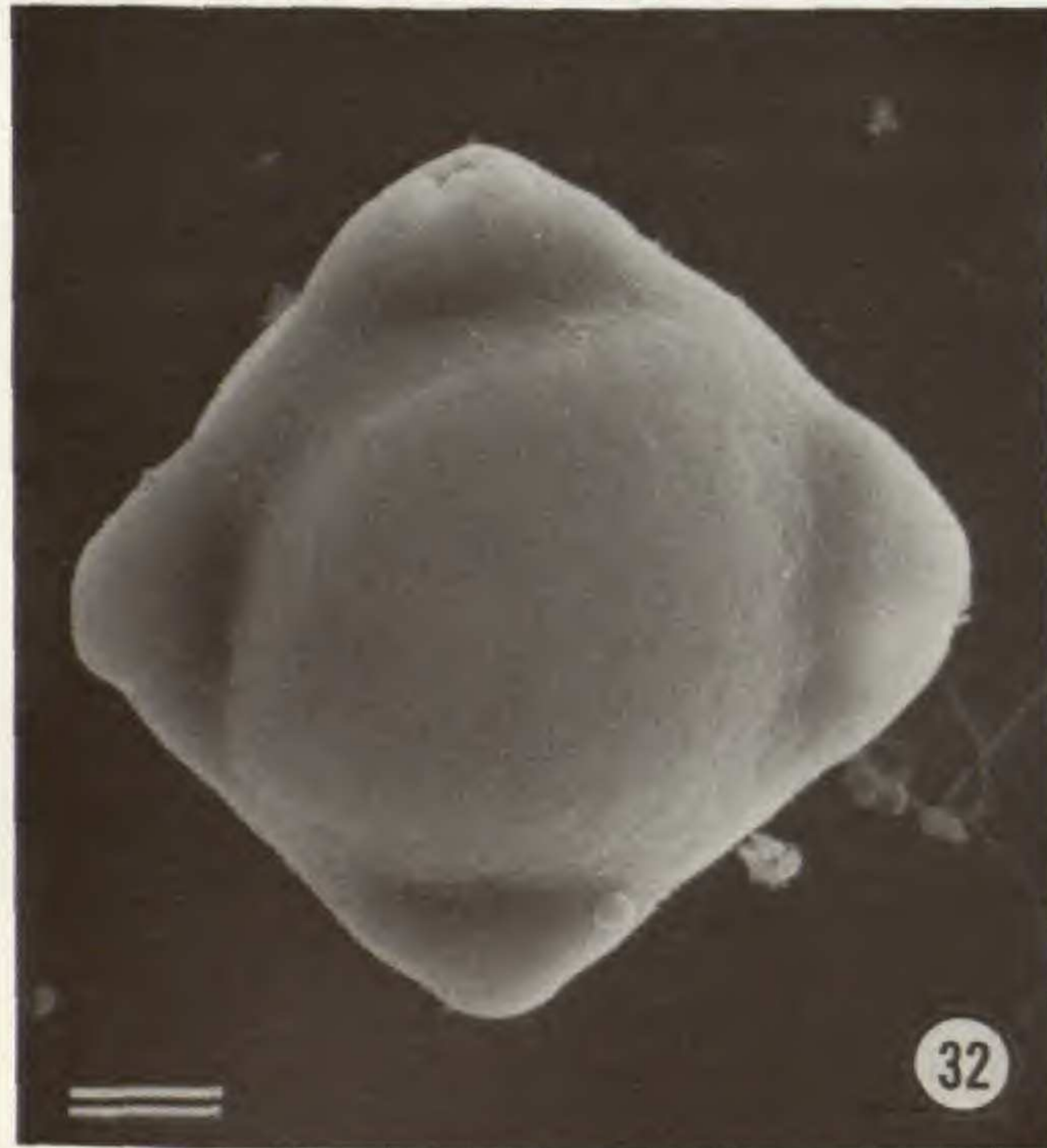
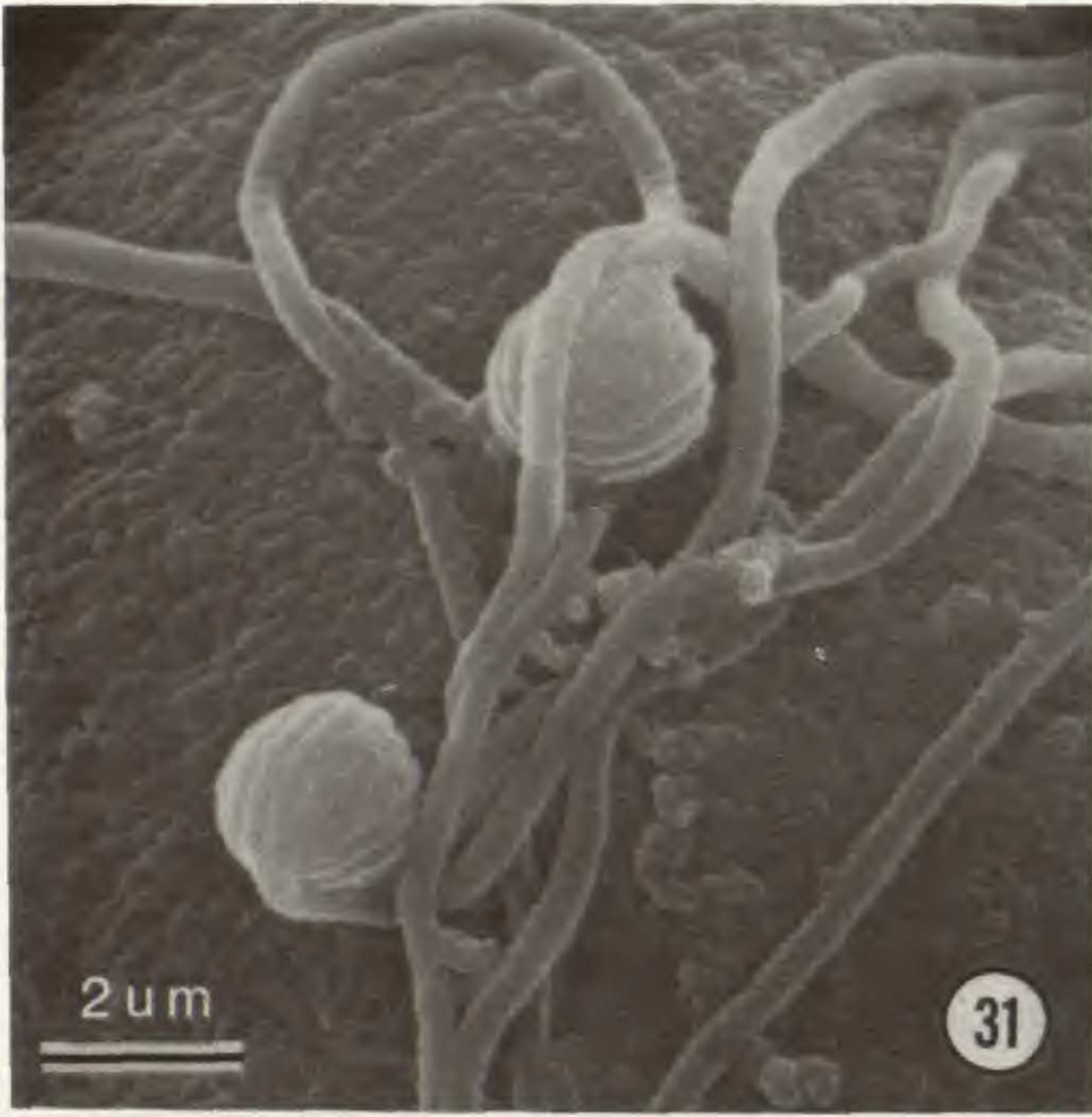
FIGURES 13–15. Scanning electron micrographs of *Fuchsia* sect. *Ellobium*, *F. splendens*.—13. Slightly oblique polar view.—14. Proximal pole with attached threads.—15. Exine fracture illustrating spongy ektexine and massive, solid endexine. The scale equals 2 μm , unless indicated.

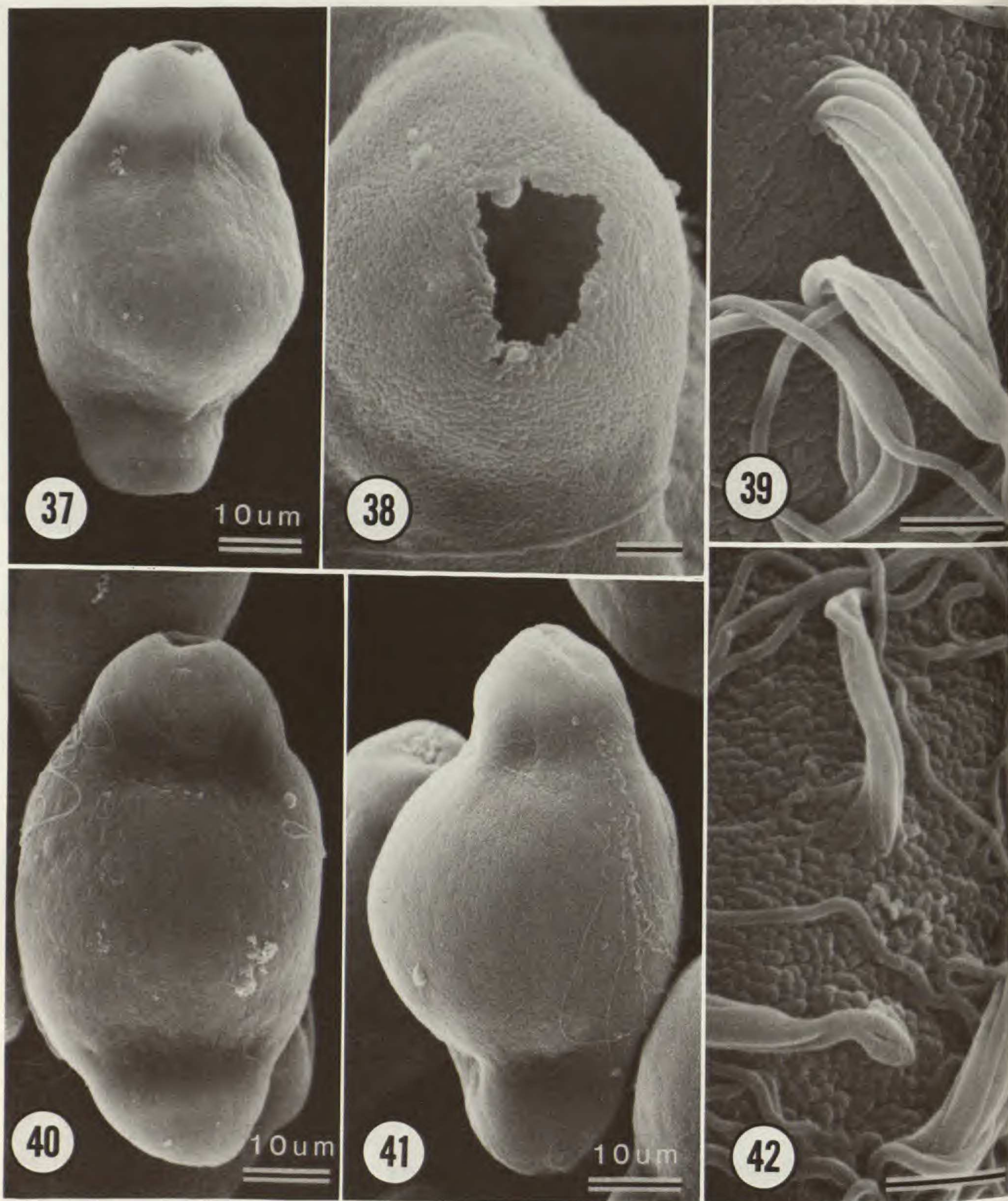


FIGURES 16-21. Scanning electron micrographs of *Fuchsia* sect. *Quelusia*.—16. *F. regia*, low magnification of group. 17, 18. *F. bracedlinae*.—17. Proximal polar view.—18. Aperture-centered equatorial view.—19. *F. campos-portoi*, polar view. 20, 21. *F. magellanica*.—20. Slightly oblique distal polar view.—21. Aperture-centered equatorial view. The scale equals 10 μm .

FIGURES 22-30. Scanning electron micrographs of *Fuchsia* sect. *Quelusia*.—22-24. *F. magellanica*, variation in thread attachment and ectexine sculpture within a sample, all threads segmented.—25. *F. campos-portoi*, segmented viscin threads. 26-30. *F. regia*.—26-27. Segmented viscin thread.—28. Pore.—29. Note the high density of threads in some grains.—30. Segmented viscin threads. The scale equals 2 μm .

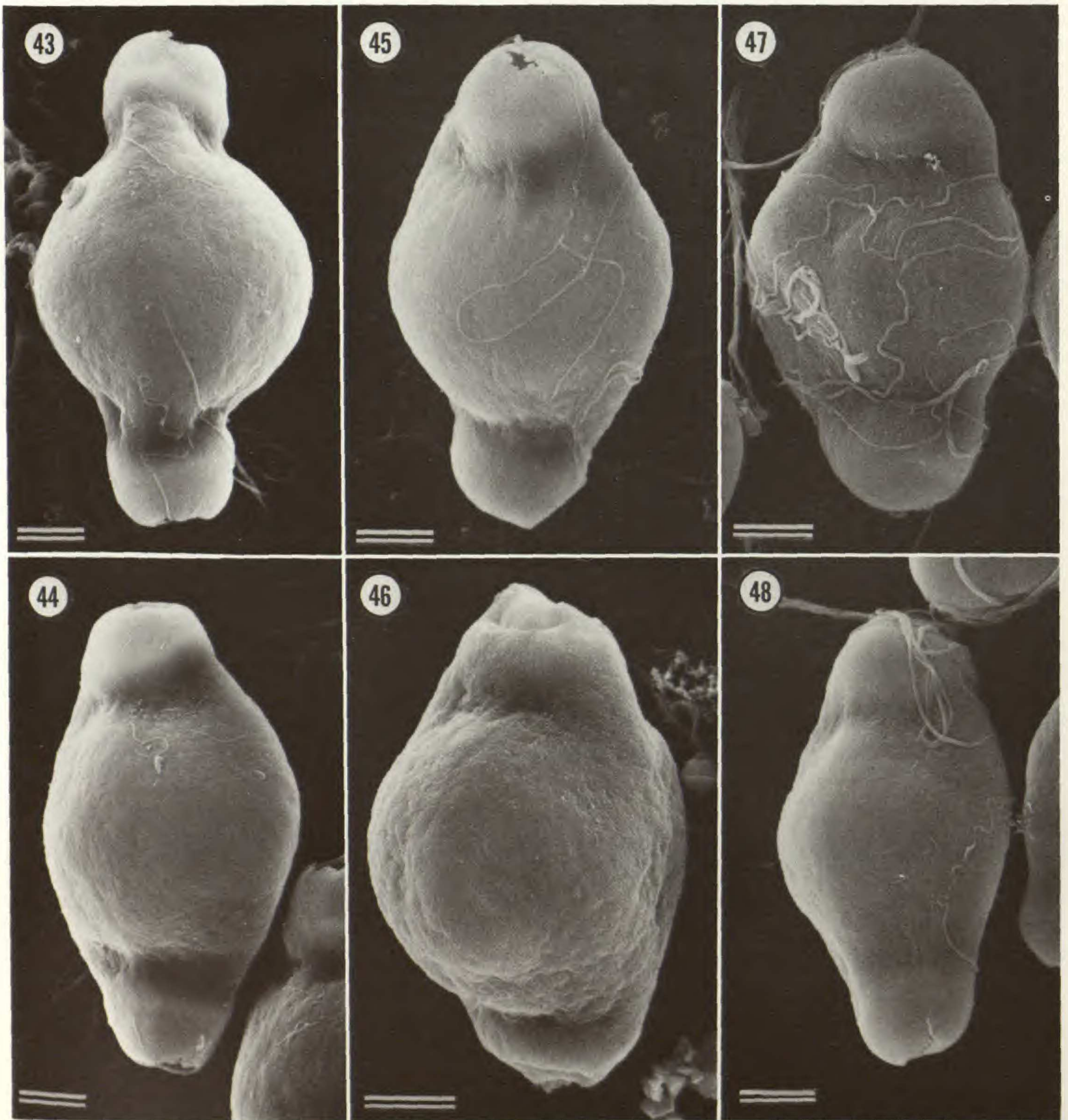




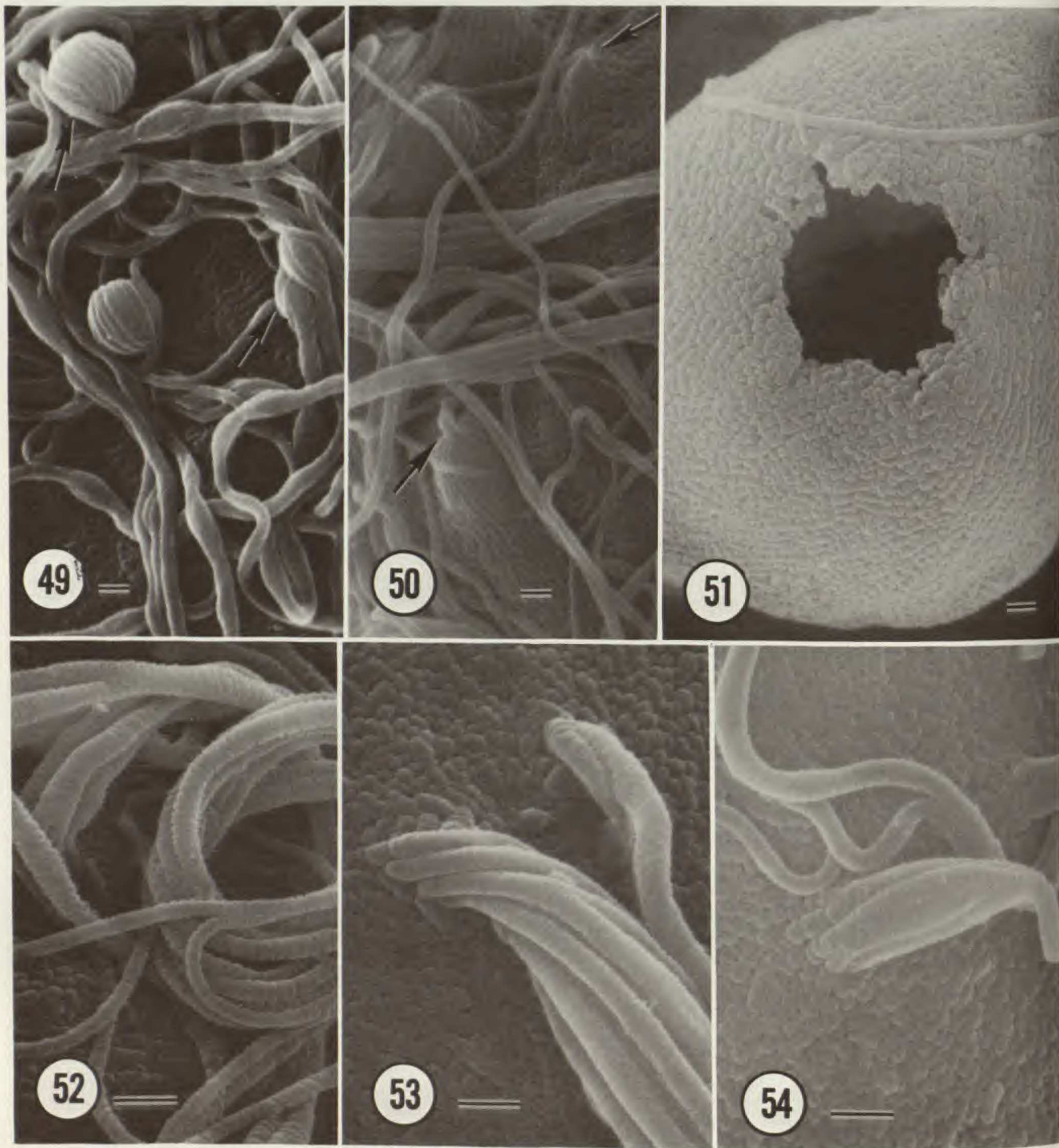


FIGURES 37-42. Scanning electron micrographs of *Fuchsia* sect. *Schufia*. 37-40. *F. arborescens*.—37. Slightly oblique polar view.—38. Pore with ragged margin.—39. Smooth to slightly segmented (?) viscin threads with an ektexine sculpture of both globular and elongated elements.—40. Polar view. 41, 42. *F. paniculata*.—41. Slightly oblique view.—42. See legend of Figure 39. The scale equals 2 μm , unless indicated.

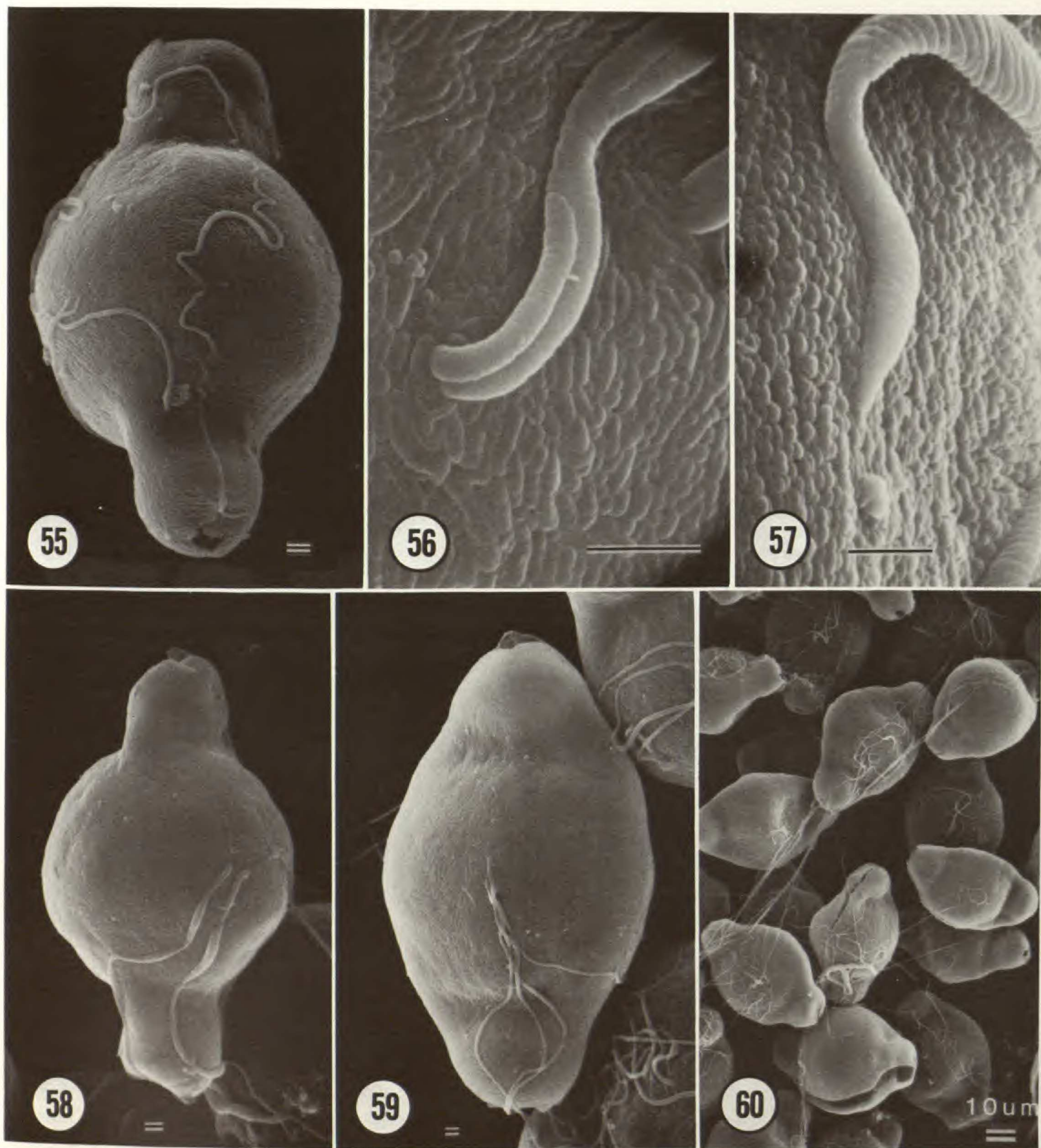
←
 FIGURES 31-36. Scanning electron micrographs of *Fuchsia* sect. *Quelusia*. 31-33. *F. coccinea*.—31. Segmented viscin threads showing localized nodular distensions (see also Fig. 49).—32. A 4-aperturate grain, polar view.—33. Slightly oblique polar view. 34-36. *F. regia*.—34. Group of 3-aperturate grains.—35. Equatorial fracture, note thickened endexine around endoapertures.—36. Slightly oblique polar view. The scale equals 10 μm , unless indicated.



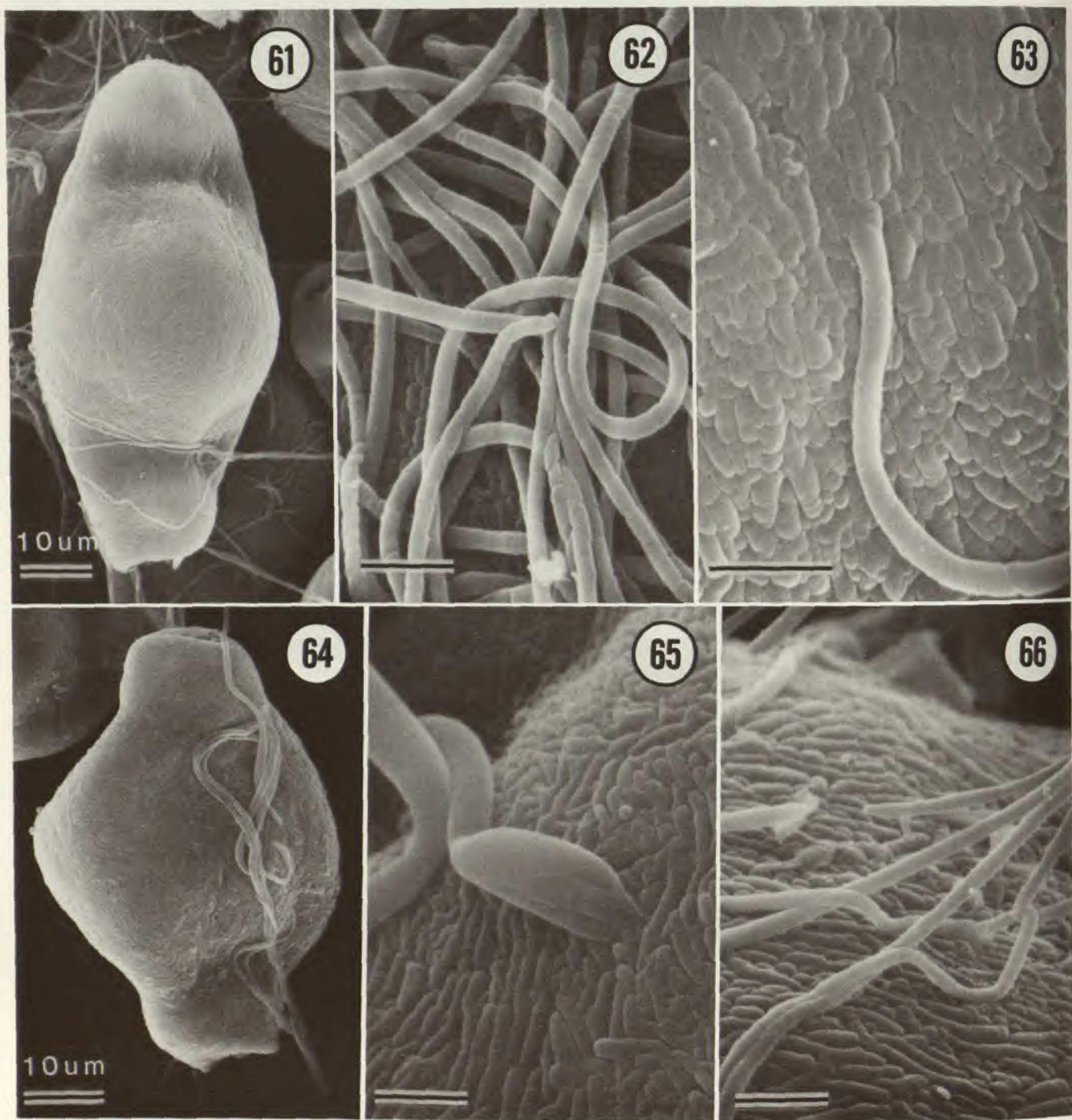
FIGURES 43–48. Scanning electron micrographs of *Fuchsia* sect. *Skinnera*. 43, 44. *F. excorticata*.—43. Mesocolpus-centered equatorial view.—44. Slightly oblique polar view.—45. *F. perscandens*, oblique polar view.—46. *F. cyrtandroides*, mesocolpus-centered equatorial view. 47, 48. *F. procumbens*.—47. Slightly oblique proximal polar view.—48. Slightly oblique polar view. The scale equals 10 μm .



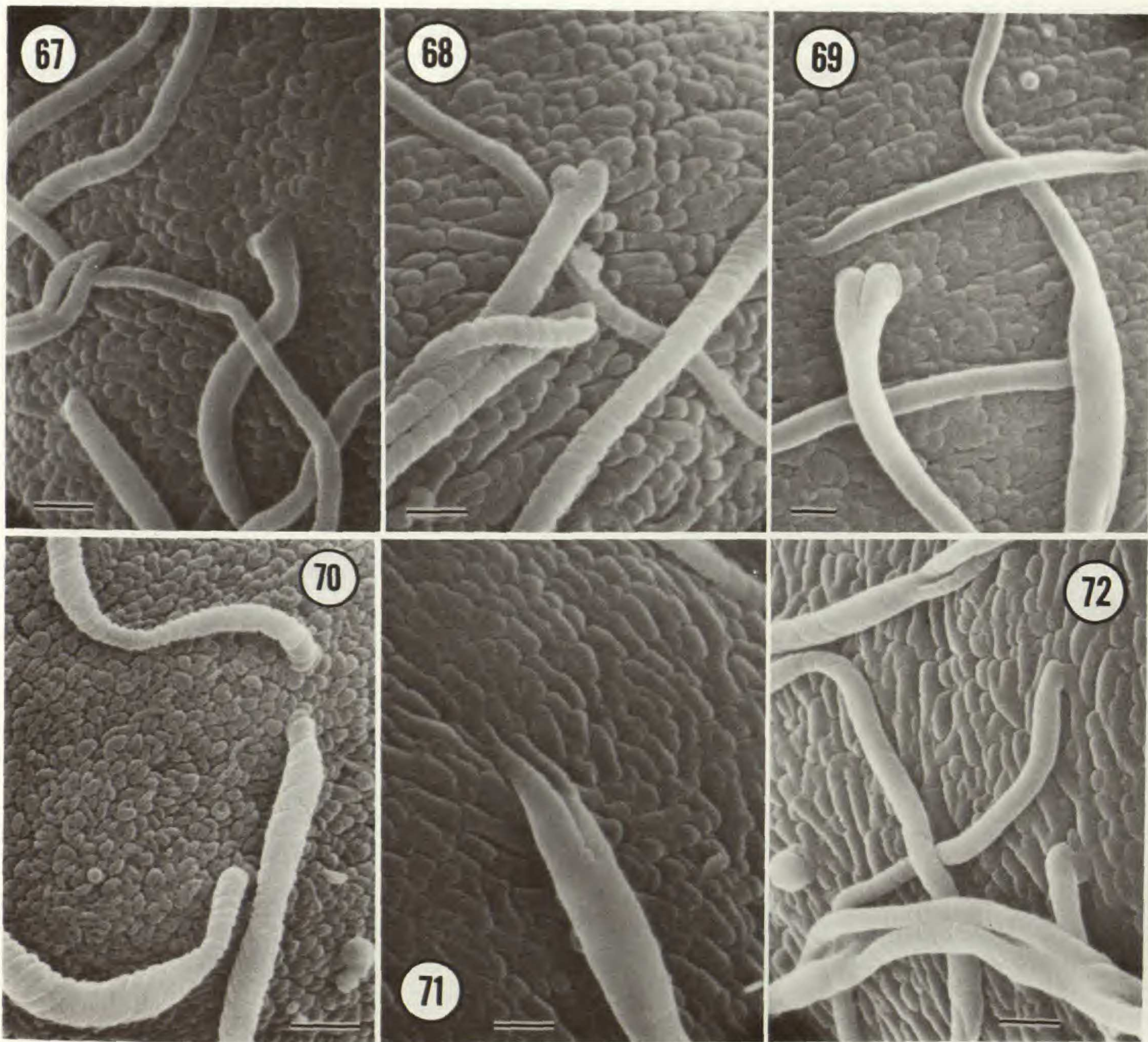
FIGURES 49–54. Scanning electron micrographs of *Fuchsia* sect. *Skinnera*. 49–50. *F. cyrtandroides*.—49. Viscin threads with various sized nodular distensions (arrows).—50. Ektexine at proximal pole with attachment of threads from inflated bases with somewhat elongated surface elements (arrows). Note that at this magnification (also Fig. 49) viscin threads appear to be mostly smooth with only rare suggestions of light segmentation; these should be compared with transmission electron micrographs (Figs. 183, 184) and companion high magnification scanning electron micrographs (Figs. 182, 185).—51. *F. excorticata*, pore with thin, ragged margin.—52. *F. procumbens*, segmented viscin threads.—53. *F. perscandens*, attachment of multiple-stranded, segmented viscin threads with globular element sculpture.—54. *F. excorticata*, see legend of Figure 53. The scale equals 1 μm .



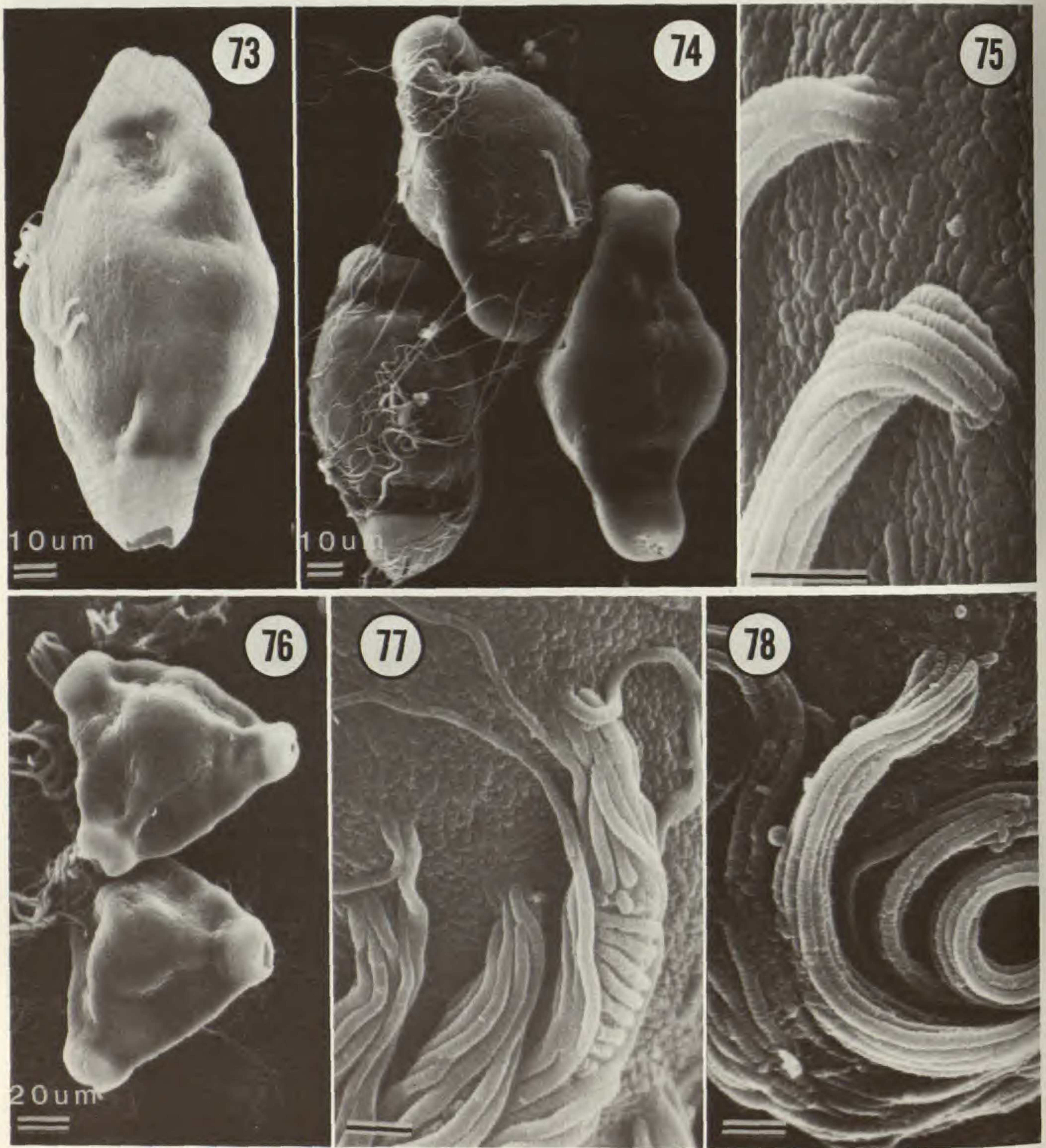
FIGURES 55–60. Scanning electron micrographs of *Fuchsia* sect. *Encliandra*. 55–57. *F. thymifolia* subsp. *thymifolia*.—55. Oblique view.—56. Ektexine with elongated element sculpture and sparsely segmented viscin threads.—57. Ektexine with globular element sculpture and segmented-ropy viscin thread (see also Fig. 147 of *F. thymifolia* subsp. *minimiflora*).—58. *F. obconica*, slightly oblique equatorial view. 59, 60, *F. encliandra* subsp. *encliandra*.—59. Proximal polar view.—60. Low magnification of group of pollen grains. The scale equals 2 μm , unless indicated.



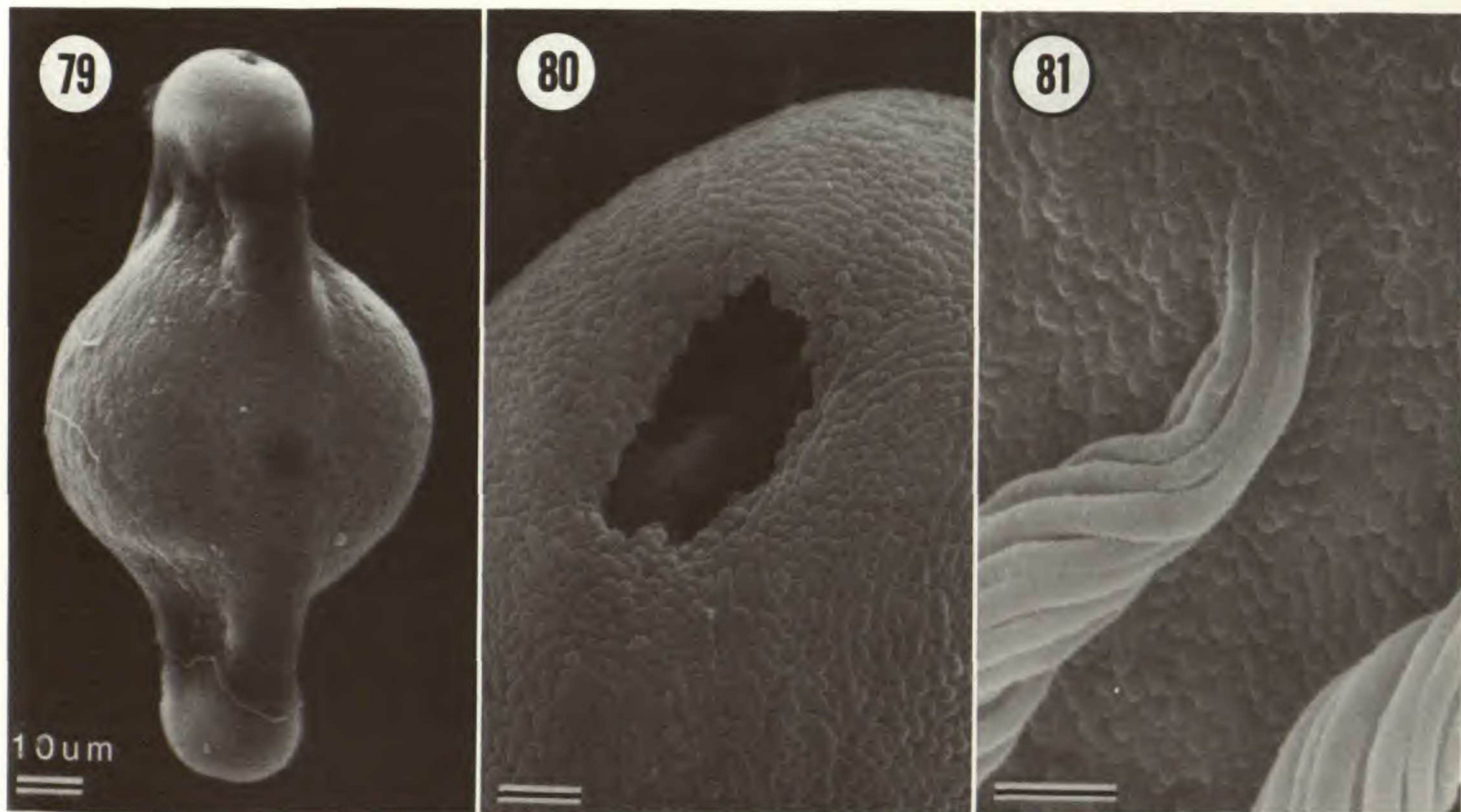
FIGURES 61–66. Scanning electron micrographs of *Fuchsia* sect. *Encliandra*. 61–63. *F. ravenii*.—61. Slightly oblique polar view.—62. Sparsely segmented threads.—63. Ectexine with elongated elements and smooth threads. 64, 65. *F. microphylla* subsp. *hemsleyana*.—64. Slightly oblique proximal polar view.—65. Ectexine with elongated elements and smooth threads.—66. *F. microphylla* subsp. *microphylla*, see legend of Figure 65. The scale equals 2 μm, unless indicated.



FIGURES 67–72. Scanning electron micrographs of *Fuchsia* sect. *Encliandra*. Viscin threads.—67. *F. cylindracea*, very sparsely segmented threads, with globular-elongated element sculpture.—68. *F. thymifolia* subsp. *thymifolia*, very sparsely segmented threads, with globular-elongated element sculpture.—69. *F. encliandra* subsp. *encliandra*, smooth threads.—70. *F. obconica*, segmented viscin threads, ectexine with globular element sculpture.—71. *F. ravenii*, viscin thread forked at exine surface and then inflated and smooth in area immediately adjacent; other parts of thread are segmented-ropy (upper right corner).—72. *F. cylindracea*, sparsely segmented threads with elongated element sculpture. The scale equals 1 μm .



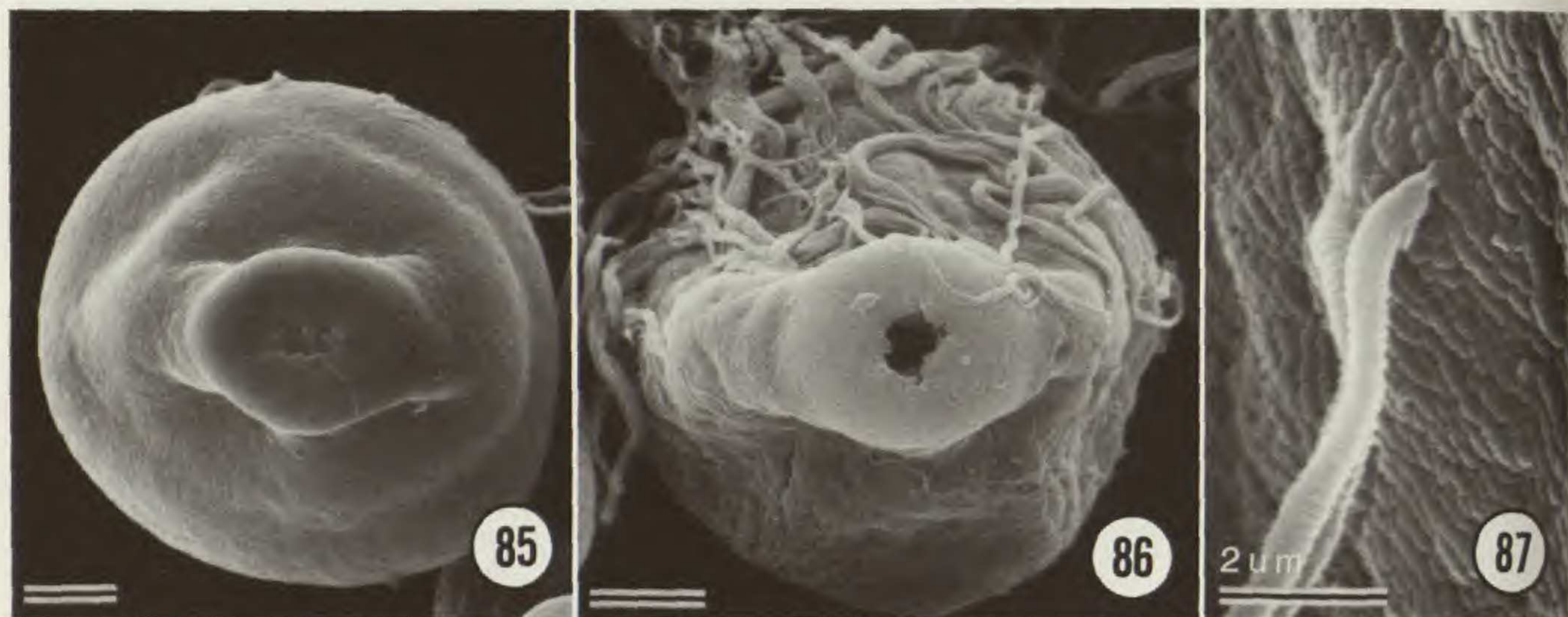
FIGURES 73–78. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*. 73–75. *F. apetala*.—73. Oblique view.—74. Low magnification of group.—75. Ektexine with globular element sculpture and segmented viscin threads.—76. *F. inflata*, this collection (*Berry & Aronson 3012*) had grains that were predominantly 3-aperturate; a second collection (*Berry 3038*) was predominantly 2-aperturate. In Figure 76, and to some extent those in Figures 73 and 74, the partially collapsed condition indicates a thickening around the equator of the grain.—77. *F. tillettiana*, see description of Figure 75.—78. *F. apetala*, see description of Figure 75. The scale equals 2 μm , unless indicated.



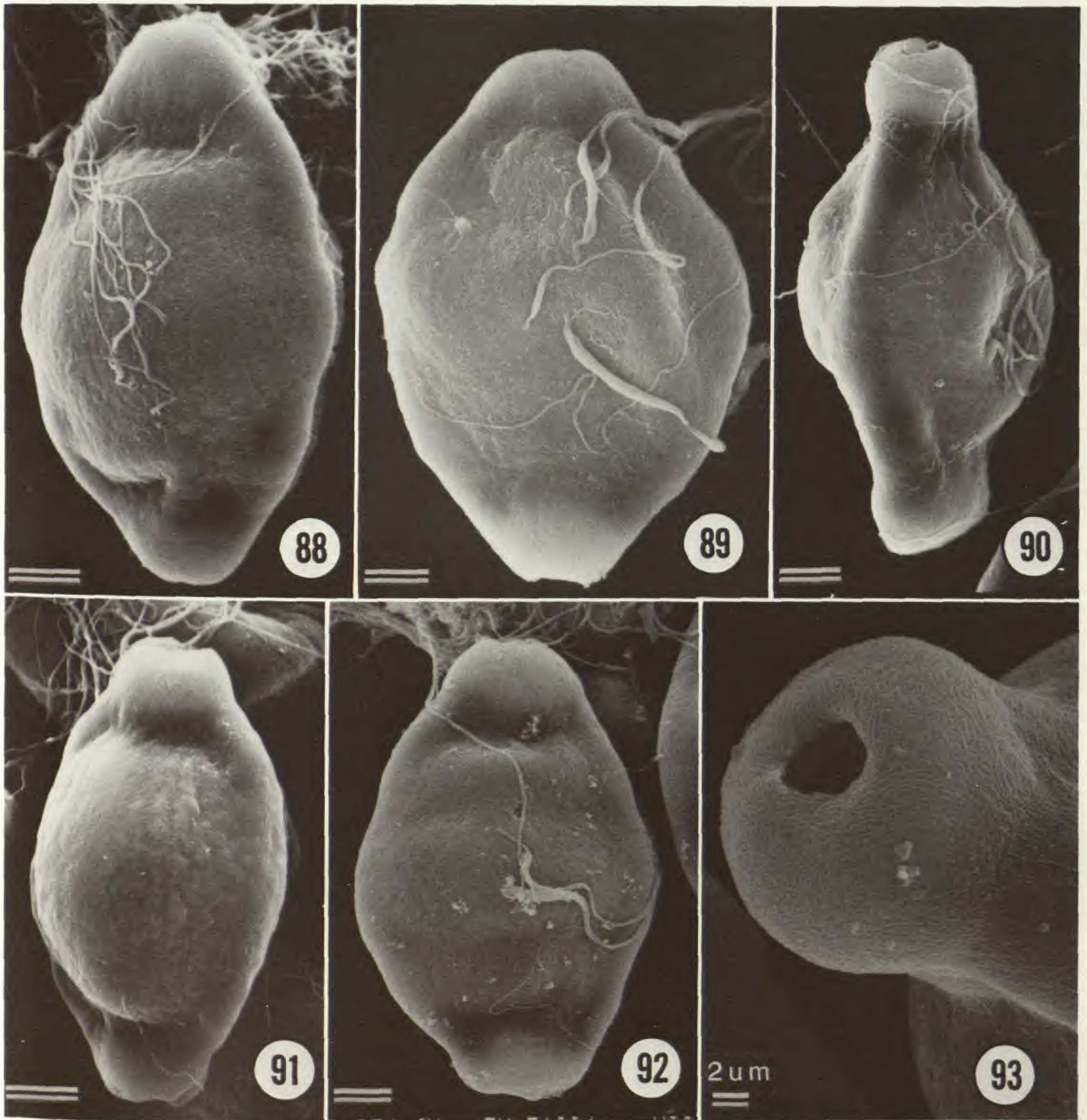
FIGURES 79–81. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*, *F. tillettiana*.—79. Slightly oblique mesocolpus-centered equatorial view, equatorial thickening (see also Figs. 73, 74, 76) is very prominent.—80. Pore.—81. Ektexine with globular sculpture element and segmented threads. The scale equals 2 μm , unless indicated.



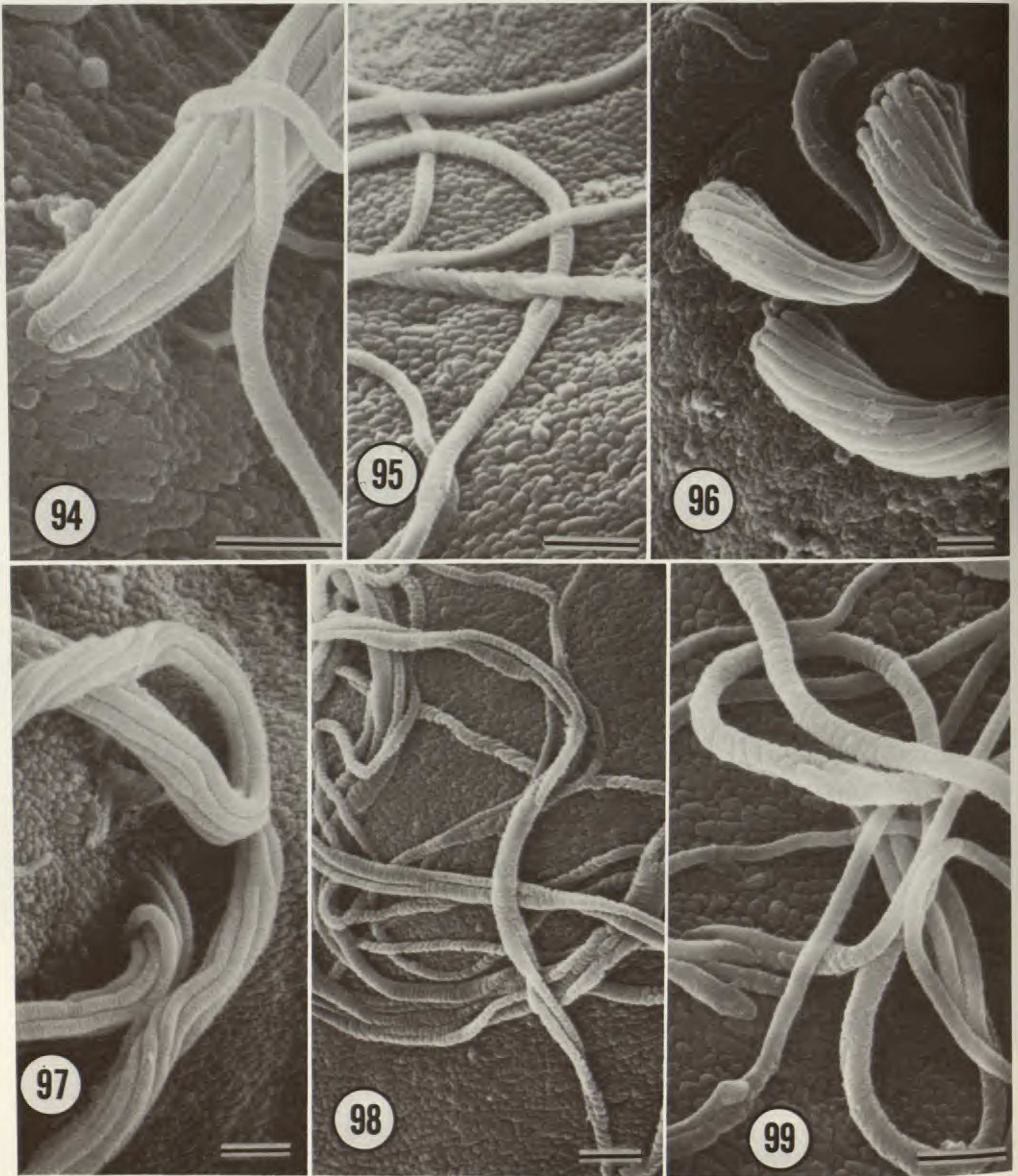
FIGURES 82–84. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*.—82. *F. chloroloba*, oblique view.—83. *F. juntasensis*, oblique view.—84. *F. apetala*, mesocolpus-centered equatorial view. The scale equals 10 μm .



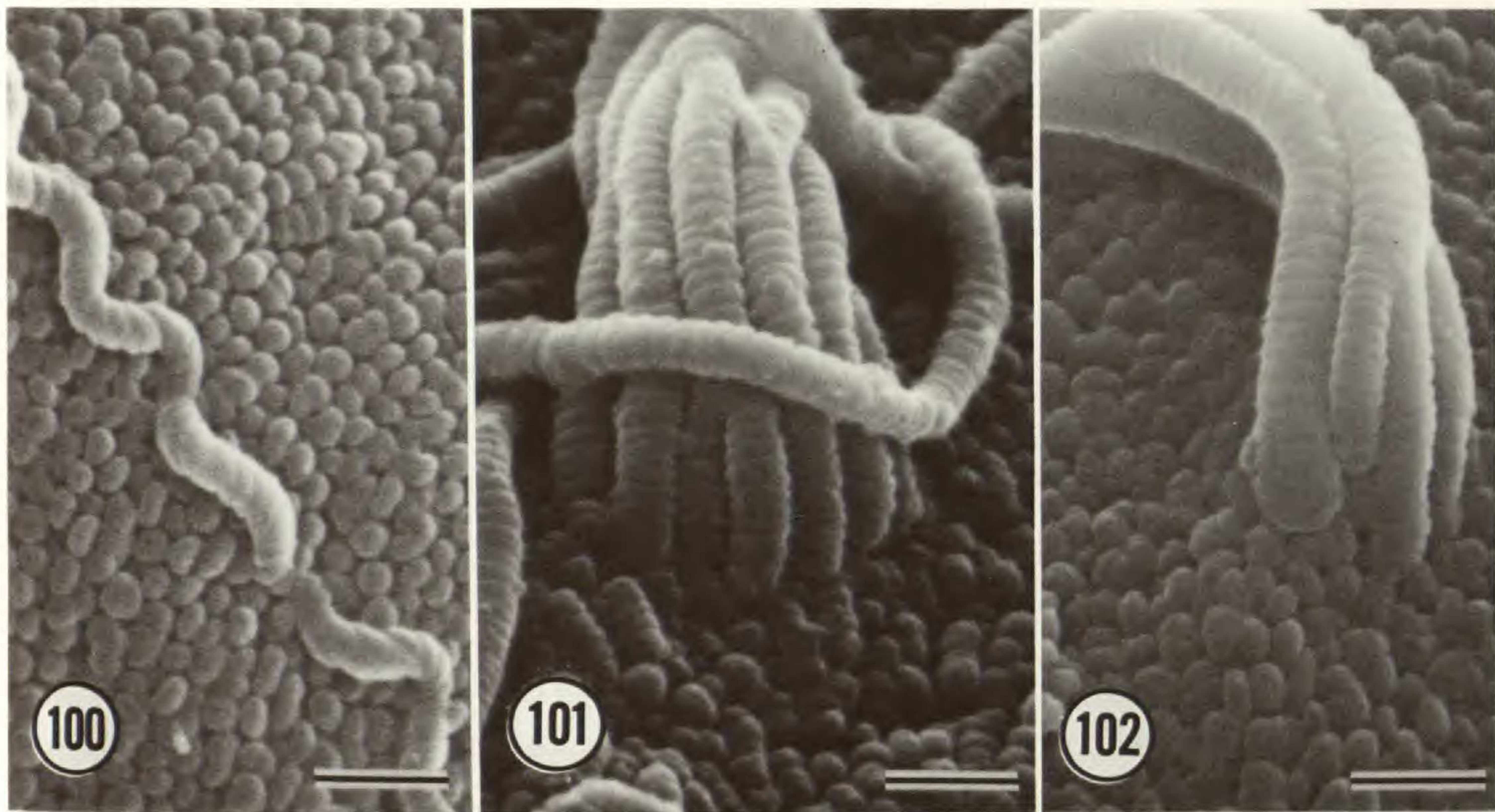
FIGURES 85–87. Scanning electron micrographs of *Fuchsia* sect. *Hemsleyella*.—85. *F. membranacea*, aperture-centered equatorial view, note elliptical shape of vestibulum. 86, 87. *F. chloroloba*.—86. Aperture-centered equatorial view.—87. Ectexine with globular element sculpture and segmented viscin threads. The scale equals 10 μm , unless indicated.



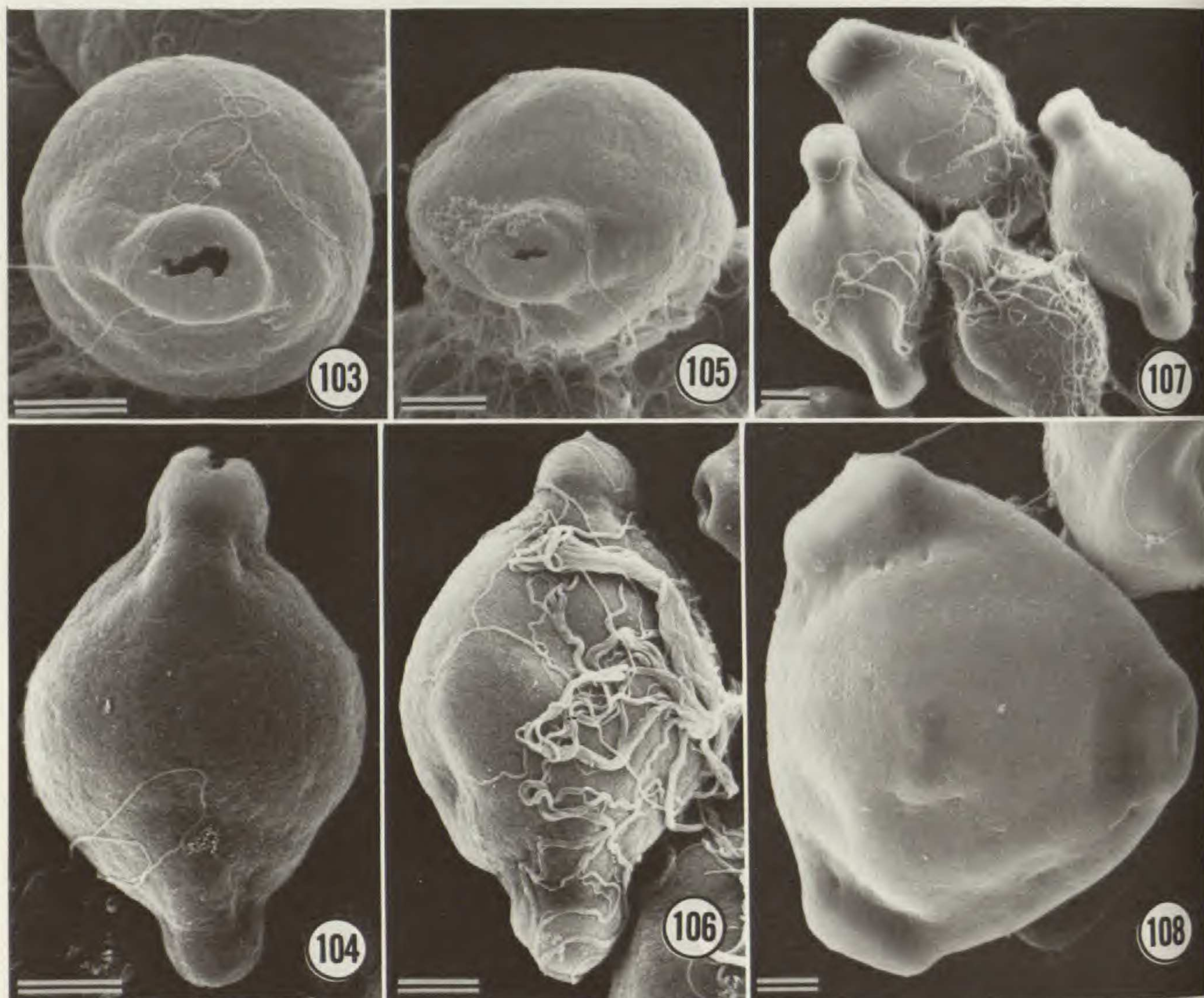
FIGURES 88–93. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*.—88. *F. triphylla*, slightly oblique proximal polar view.—89. *F. pringsheimii*, proximal polar view.—90. *F. gehrigeri*, oblique view.—91. *F. ayavacensis*, oblique distal view. 92, 93. *F. macrostigma*.—92. Proximal polar view.—93. Aperture, oblique view. The scale equals 10 μm , unless indicated.



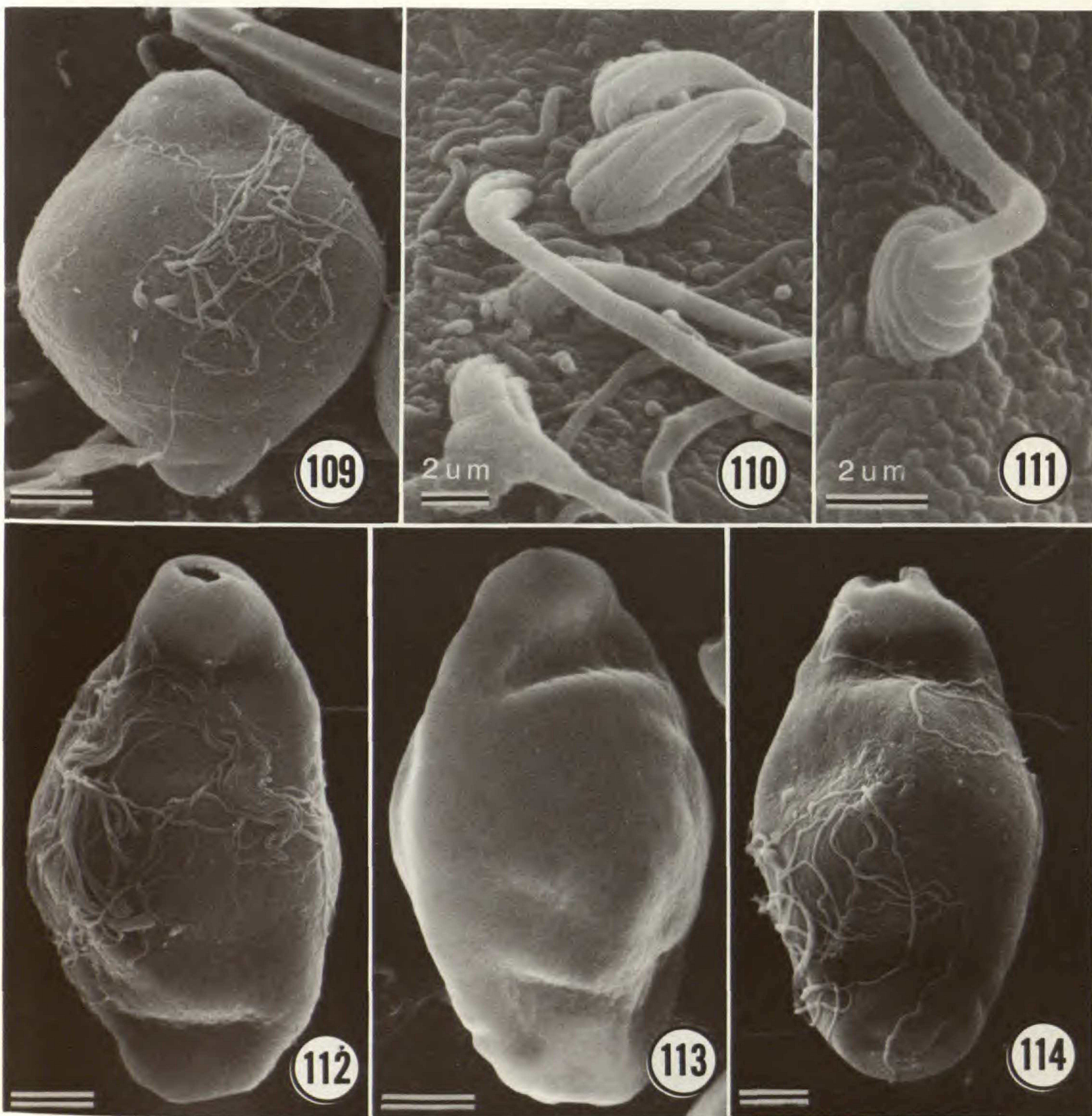
FIGURES 94-99. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. Globular element sculpture with segmented viscin threads.—94. *F. triphylla*.—95. *F. hirtella*.—96. *F. gehrigeri*.—97. *F. cuatrecasasii*.—98. *F. pallescens*.—99. *F. petiolaris*. The scale equals 2 μm .



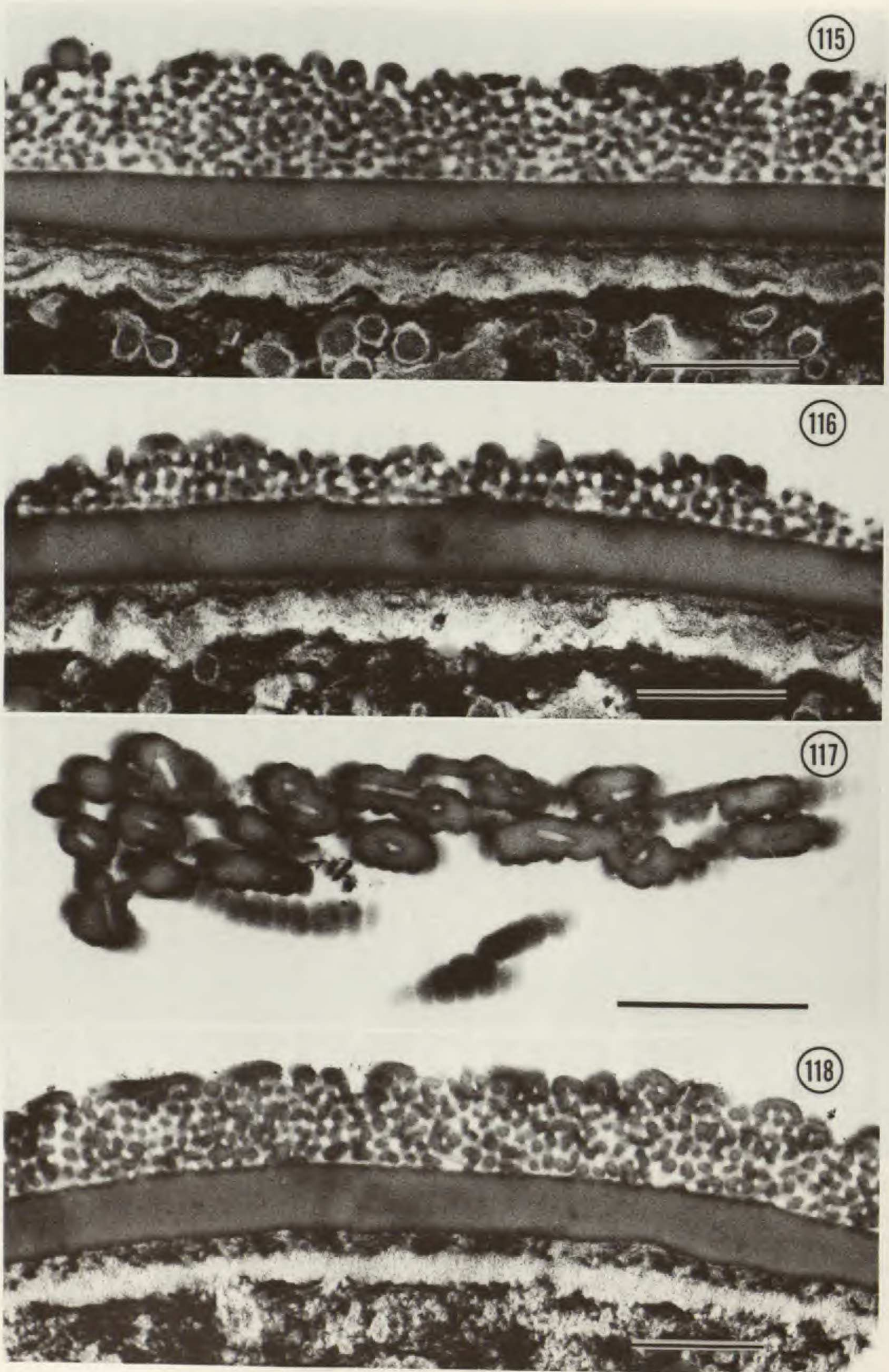
FIGURES 100–102. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. Globular element sculpture with segmented viscin threads.—100. *F. tincta*.—101. *F. boliviana*.—102. *F. putumayensis*. The scale equals 1 μm .



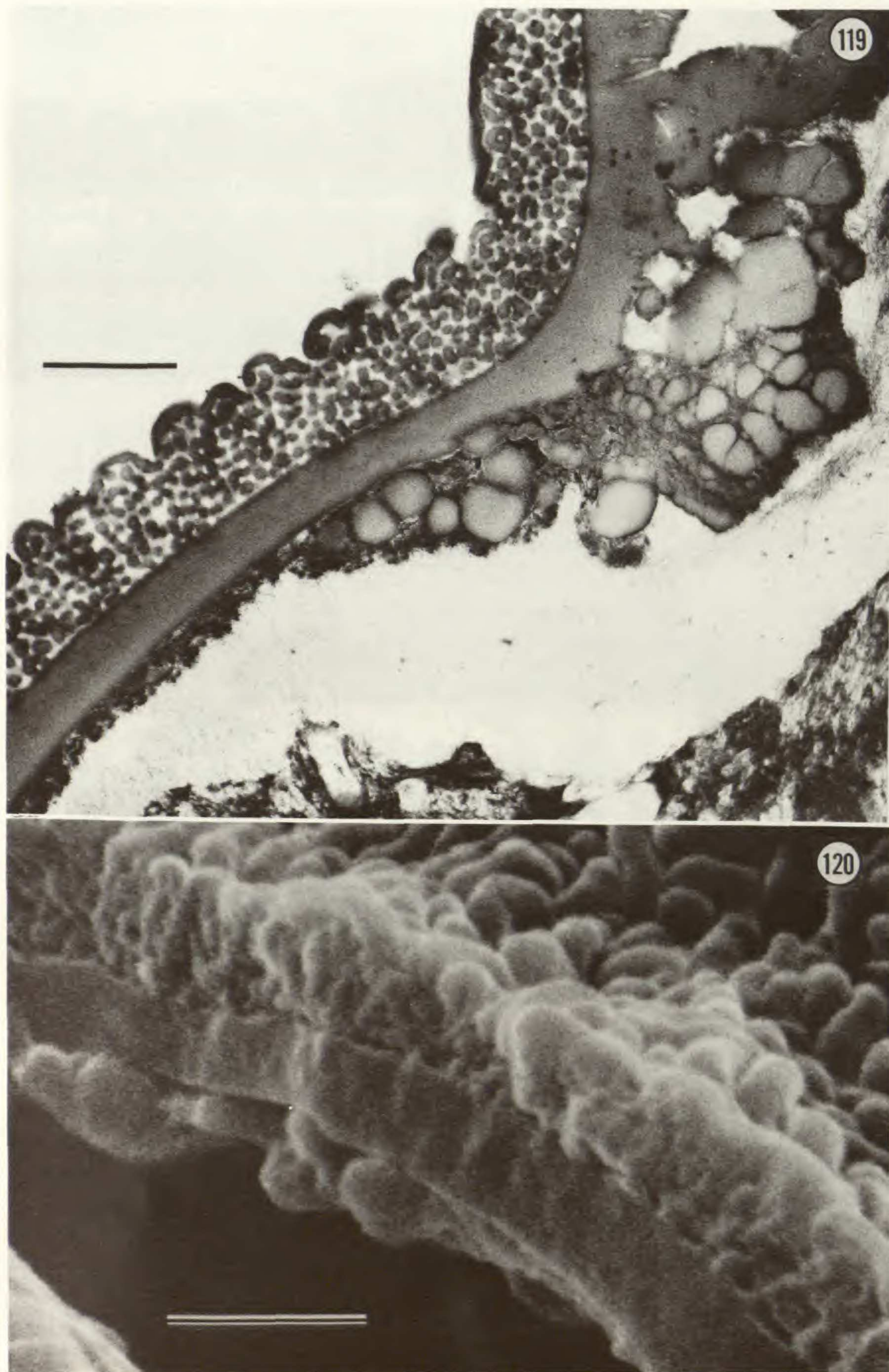
FIGURES 103–108. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. 103–104. *F. macrophylla*.—103. Aperture-centered equatorial view, colpus slightly distorted.—104. Mesocolpus-centered equatorial view. 105, 106. *F. tincta*.—105. Aperture-centered equatorial view.—106. Mesocolpus-centered equatorial view.—107. *F. scabriuscula*, four grains held together by threads.—108. *F. corollata*, a 3-aperturate grain. The scale equals 10 μm .



FIGURES 109–114. Scanning electron micrographs of *Fuchsia* sect. *Fuchsia*. 109–111. *F. verrucosa*.—109. Proximal polar view.—110. Smooth viscin threads with irregular sculpture.—111. See legend of Figure 110.—112. *F. hartwegii*, oblique polar view.—113. *F. mathewsii*, distal polar view.—114. *F. petiolaris*, proximal polar view. Unless indicated, the scale equals 10 μm .



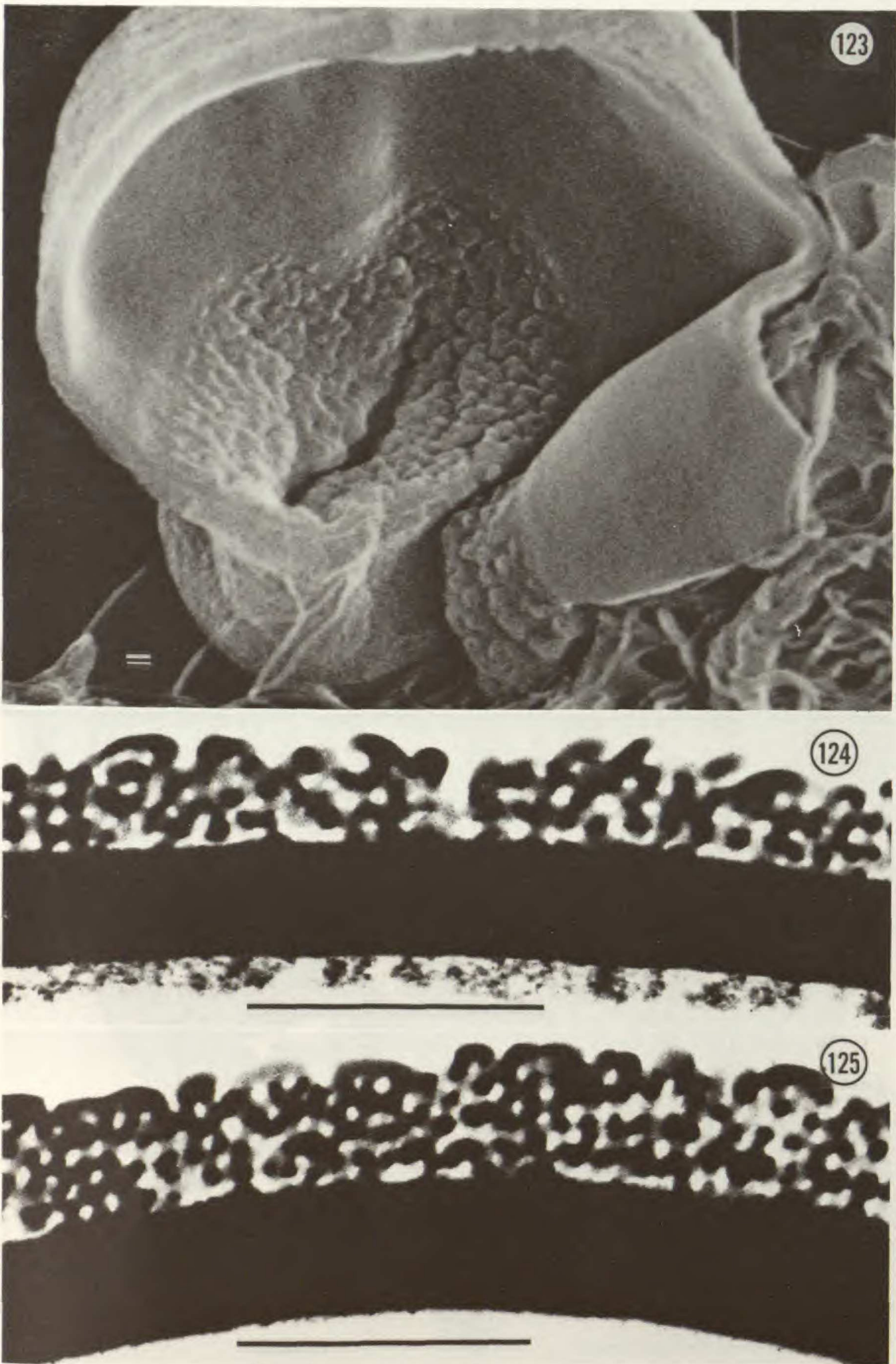
FIGURES 115-118. Transmission electron micrographs of *Fuchsia* pollen, sect. *Ellobium* (Figs. 115-117) and sect. *Encliandra* (Fig. 118). All pollen rehydrated. 115-117. *F. splendens*.—115. Section from approximately the middle of the distal polar face (at right) to the junction of the central body and apertural protrusion (tapered part of the endexine at left).—116. Same pollen grain as in Figure 115 but section from directly opposite polar face (i.e., proximal). Note the comparatively thinner ectexine.—117. Section through numerous viscin threads.—118. *F. ravenii*, section through middle of central body. In contrast to Figures 115 and 116 the granular basal component of the endexine forms a fairly uniform zone or layer, being clearly demarcated from the above massive endexine and below intine. The scale equals 1 μ m.



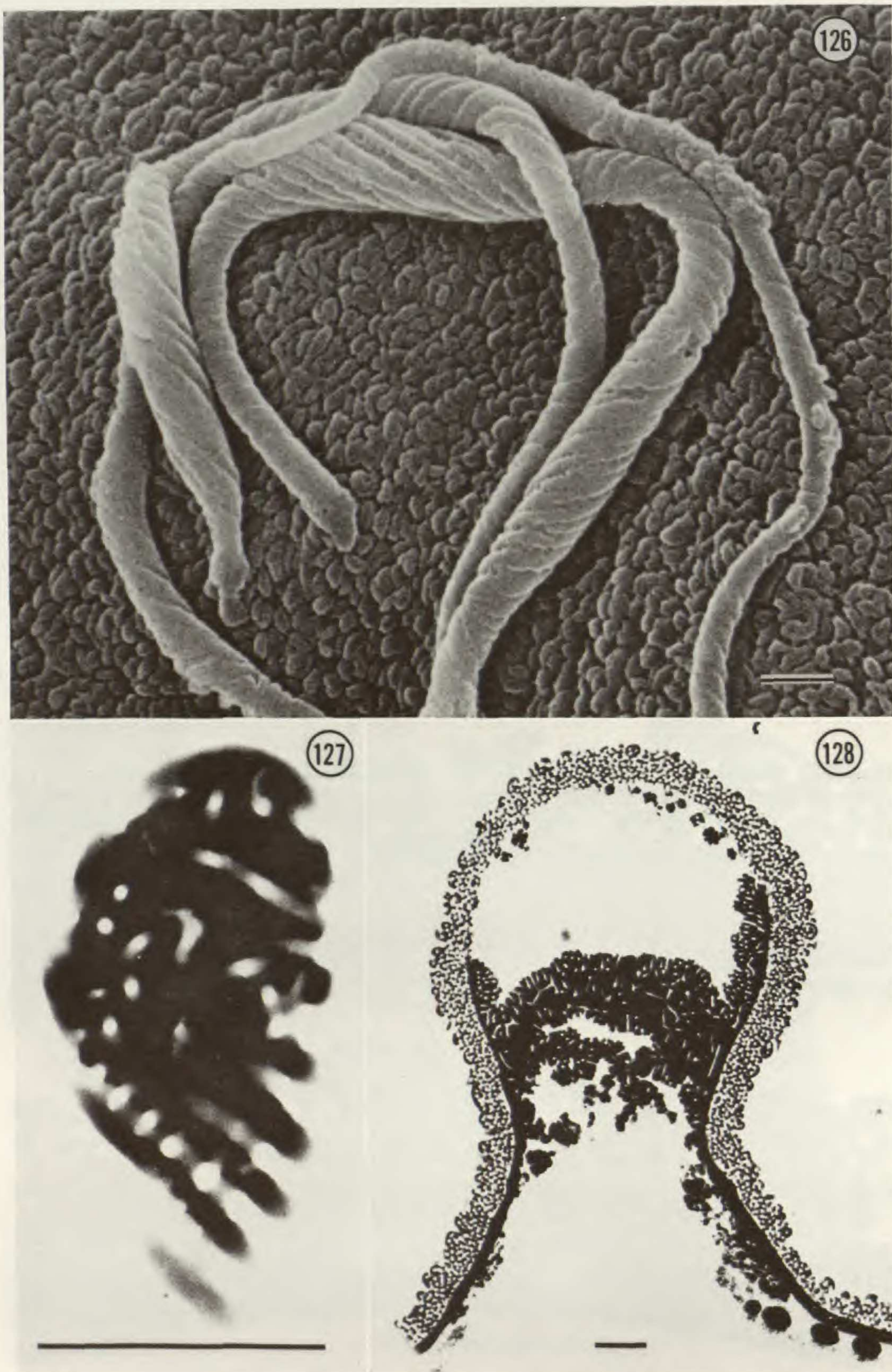
FIGURES 119, 120. Transmission (Fig. 119) and scanning (Fig. 120) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Rehydrated (Fig. 119) and acetolyzed (Fig. 120) pollen.—119. *F. ravenii*, section through portion of central body and apertural protrusion.—120. *F. microphylla* subsp. *aprica*, view of fracture at the approximate junction of apertural protrusion with the central body. Note the lack of traditional structure to the ektexine, the thick and massive-homogeneous-uniform part of the endexine, and the highly irregular lower granular endexine which is roughly equivalent to the large endexine granules in Figures 119 and 122. The scale equals 1 μ m.



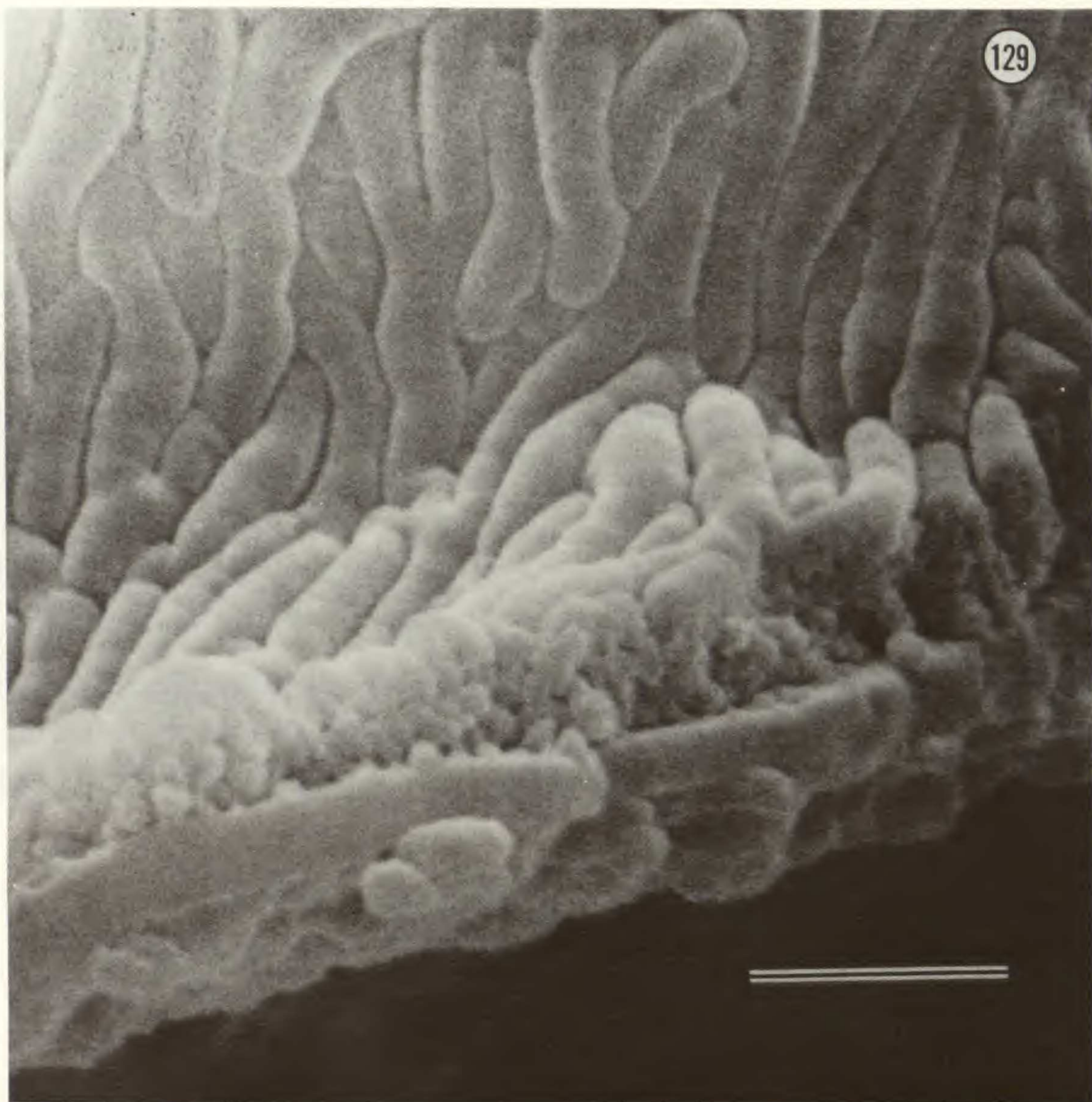
FIGURES 121, 122. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. microphylla* subsp. *aprica*. Pollen acetolyzed.—121. Section slightly off middle of central body and approaching an apertural protrusion. The acetolyzed exines of *Fuchsia* (Figs. 124, 125, 133–135, 137, 158–162, 174, 179, 194) always appear extremely opaque with both ectexine and endexine approximately of equal electron density. In contrast, the rehydrated exines (Figs. 115, 116, 118, 119, 151–154, 164–173, 175, 178, 191) with the possible exception of *F. verrucosa* (Figs. 155, 156) are considerably less dense.—122. Section of apertural protrusion, including apertural channel. Comparison of apertural protrusions in the acetolyzed (Figs. 128, 132, 136, 163, 174, 176, 177, 193) and unacetolyzed (Figs. 119, 155, 171, 191) conditions indicates direct morphological correspondences in all structural features, although the highly channeled or honeycombed endexine is more clearly distinguished after acetolysis. The scale equals 1 μm .



FIGURES 123–125. Scanning (Fig. 123) and transmission (Figs. 124, 125) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Pollen acetolyzed.—123. *F. microphylla* subsp. *aprica*, the internal view of this fractured pollen grain shows coarse globular elements of the apertural protrusion (see Figs. 119, 120) outlined by the relatively smooth endexine of the central body. 124, 125. *F. microphylla* subsp. *hidalgensis*.—124. Section near middle of the central body.—125. Same pollen grain as in Figure 124 but section from opposite face (either polar or lateral). Note absence of granular endexine component as well as slightly thicker ectexine. The scale equals 1 μm .



FIGURES 126–128. Scanning (Fig. 126) and transmission (Figs. 127, 128) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. microphylla* subsp. *hidalgensis*. Pollen acetolyzed.—126. Scanning electron micrographs of groups of twisted, segmented-ropy viscin threads similar to those observed for *F. thymifolia* subsp. *thymifolia* (see Figs. 56, 57 and Pl. 5, Fig. 1 of Skvarla et al., 1978) and *F. thymifolia* subsp. *minimiflora* (Fig. 147) and which contrast with the smooth (Fig. 131) or beaded threads more typical of *Fuchsia*.—127. Section through a group of threads.—128. Section through apertural protrusion but not including pore or aperture channel. The channeled endexine clearly underlies the vestibulum or aperture chamber. The scale equals 1 μm .



FIGURES 129, 130. Scanning (Fig. 129) and transmission (Fig. 130) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. microphylla* subsp. *hemsleyana*. Pollen acetolyzed.—129. Portion of a broken pollen grain showing the spongy undifferentiated ektexine with a surface sculpture of elongate elements. The massive endexine has a highly irregular lower margin.—130. Section through proximal surface including an oblique view of a smooth viscin thread connected with the ektexine surface. The scale equals 1 μm .

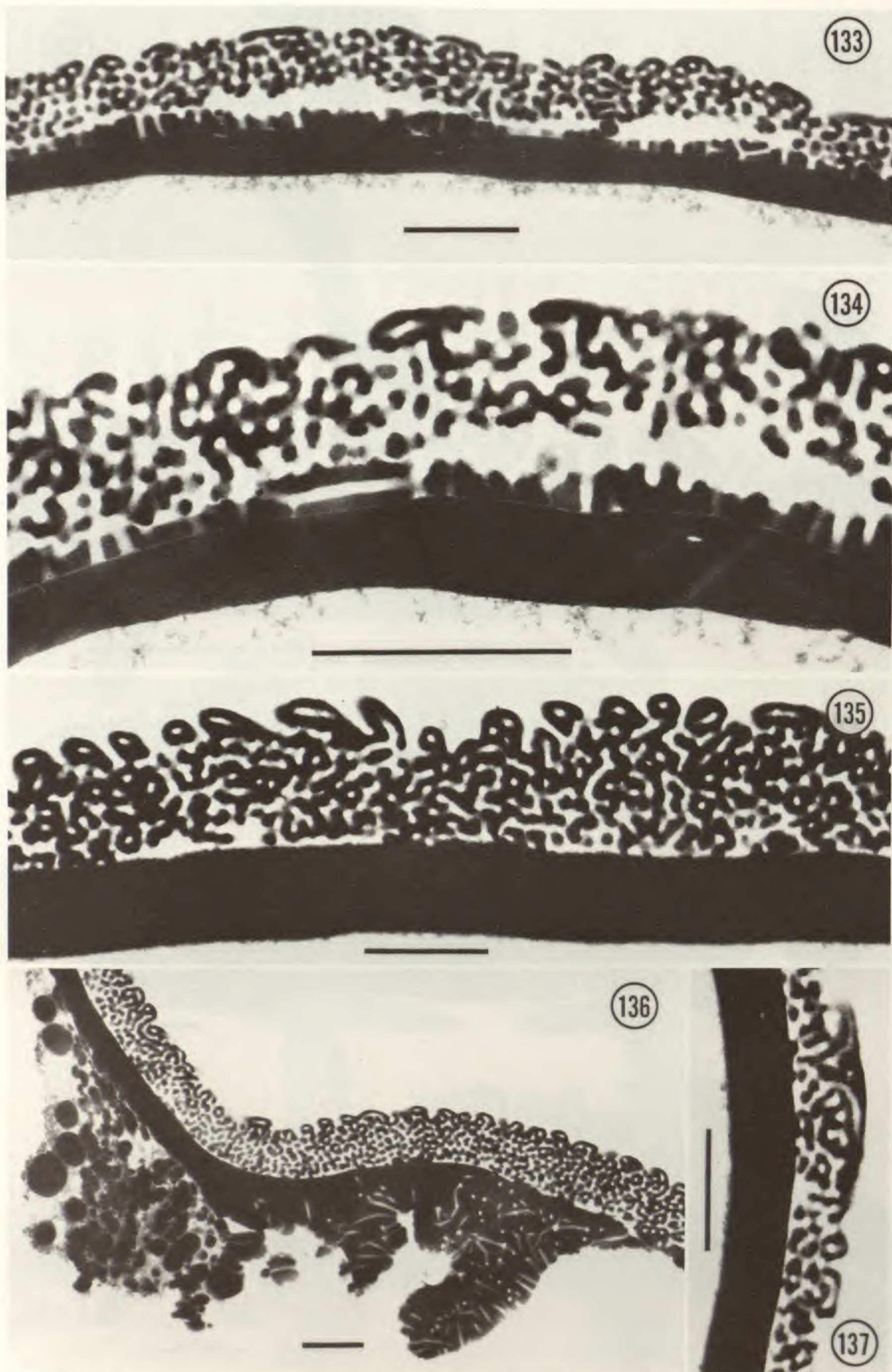


131



132

FIGURES 131, 132. Scanning (Fig. 131) and transmission (Fig. 132) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. microphylla* subsp. *quercetorum*. Pollen acetolyzed.—131. Scanning electron micrograph of a great mass of smooth viscin threads.—132. Somewhat oblique section through apertural protrusion. The scale equals 1 μ m.



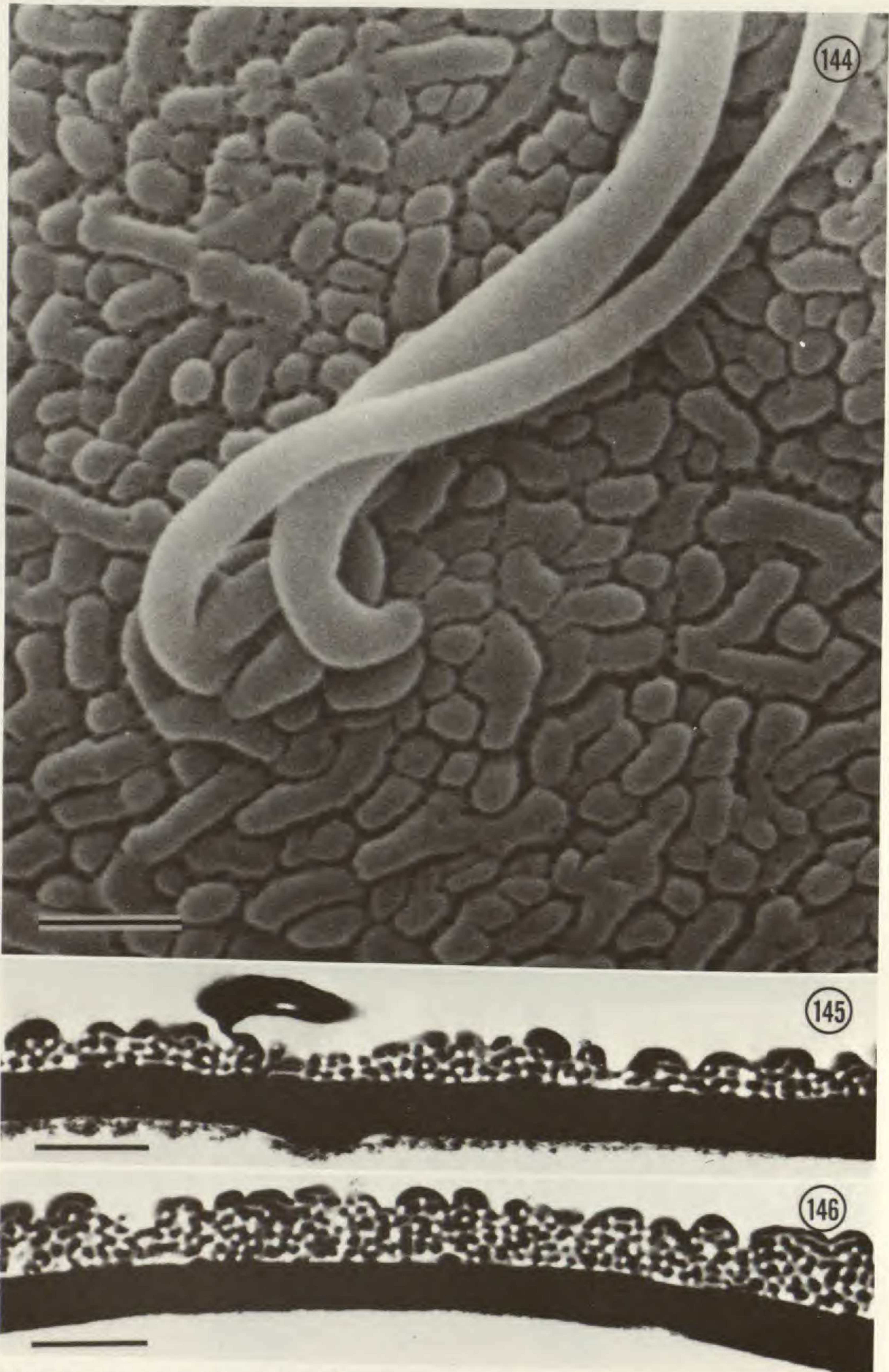
FIGURES 133–137. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra*. Pollen acetolyzed. 133, 134. *F. microphylla* subsp. *quercetorum*.—133. Section through middle of central body. Although the ektexine appears to be composed of a spongy-paracrystalline-beaded tectum separated from an irregular foot layer by occasional columellae, it seems more likely that the entire ektexine has been fractured basally. This appears to be common for this taxon (see also Pl. 1, Skvarla et al., 1976). The lower granular portion of the endexine is extensive, but in this print the fractured ektexine was emphasized at the expense of the granular endexine.—134. The same comments apply as discussed in Figure 135. 135–137. *F. encliandra* subsp. *tetradactyla*.—135. Section through middle of central body and somewhat oblique to the surface.—136. Section through portion of the central body and apertural protrusion.—137. Section near middle of central body. The structure of the ektexine (at the top) contrasts with the section in Figure 135. The scale equals 1 μm .



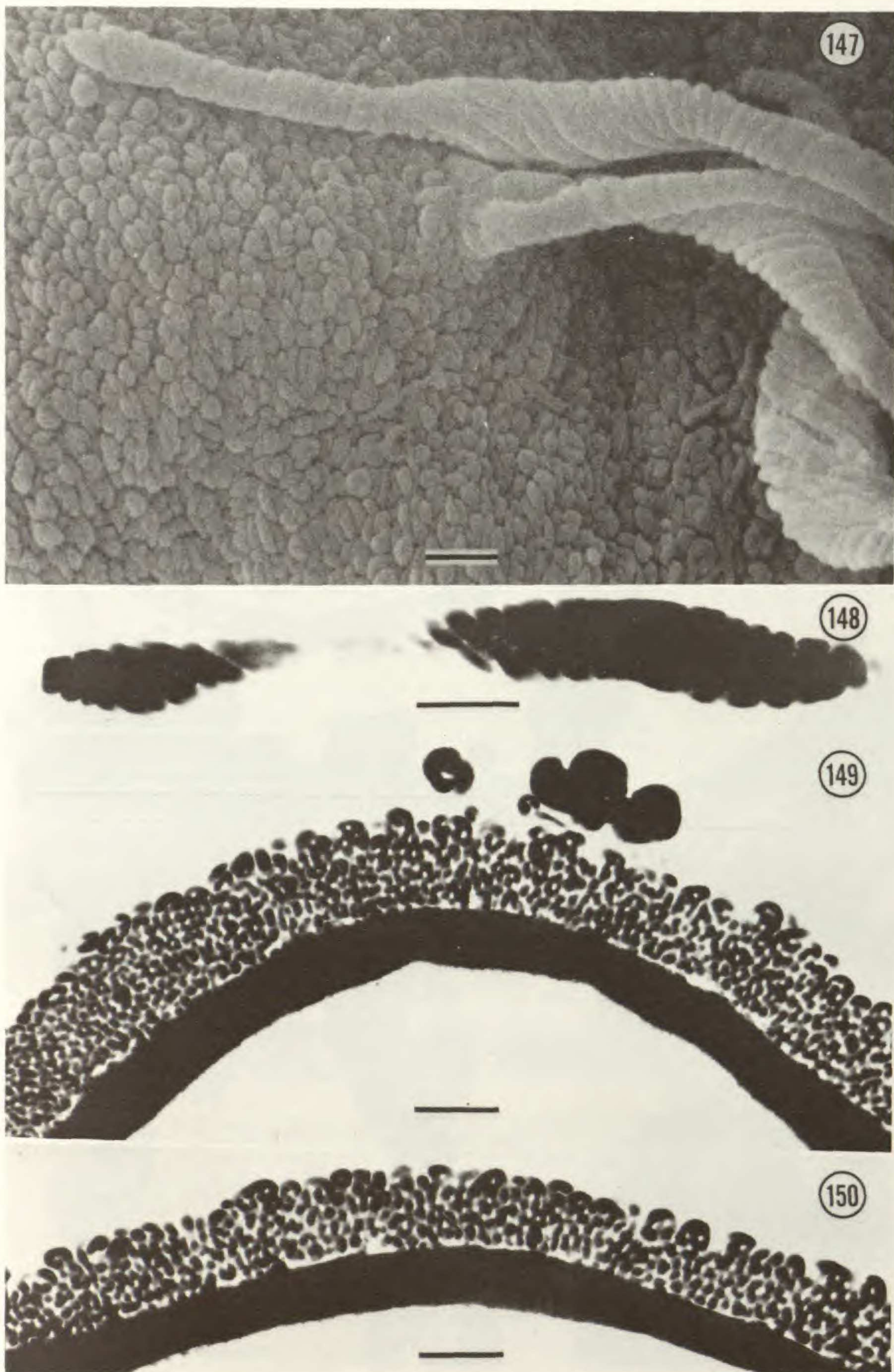
FIGURES 138-141. Transmission electron micrographs of *Fuchsia* pollen sect. *Encliandra*, *F. encliandra* subsp. *encliandra*. Pollen acetolyzed.—138. Section through proximal surface.—139. Longitudinal section through parts of two smooth viscin threads.—140. Section through a cluster of viscin threads with various orientations.—141. Somewhat oblique section through proximal surface near region of aperture protrusion. The scale equals 1 μm .



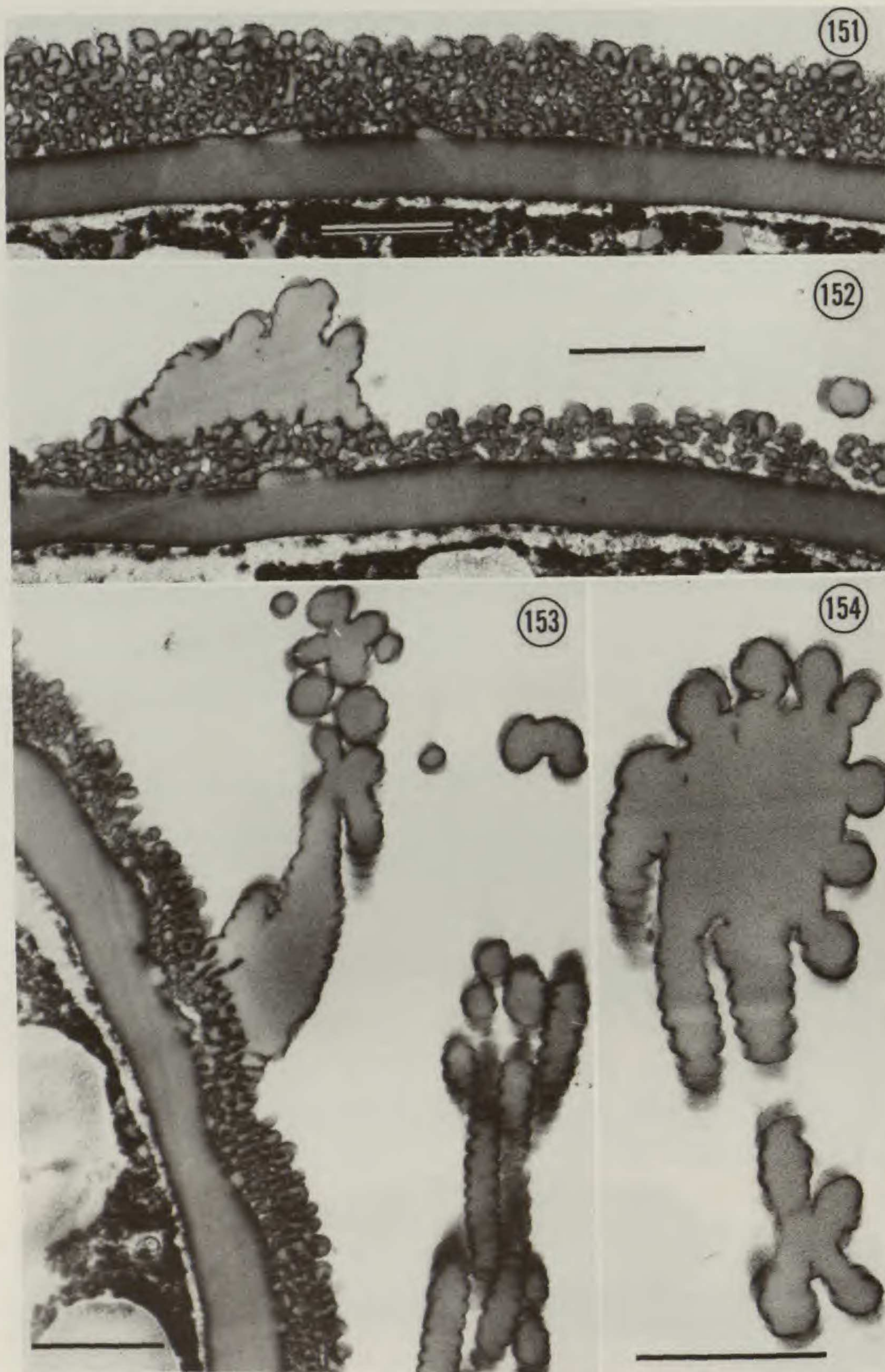
FIGURES 142, 143. Transmission electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. obconica*. Pollen acetolyzed.—142. View at proximal surface with prominently segmented viscin threads attached to exine surface.—143. Section through apertural protrusion and vestibulum but not including pore or aperture channel. The scale equals 1 μm .



FIGURES 144-146. Scanning (Fig. 144) and transmission (Figs. 145, 146) electron micrographs of *Fuchsia* pollen, sect. *Encliandra*, *F. cylindracea*. Pollen acetolyzed.—144. Smooth viscin threads are attached to the exine surface consisting mostly of slightly elongate sculpture elements.—145. Oblique view of proximal surface toward aperture protrusion with portion of a smooth viscin thread.—146. Same pollen grain section as Figure 145 but of directly opposite distal surface. The scale equals 1 μ m.



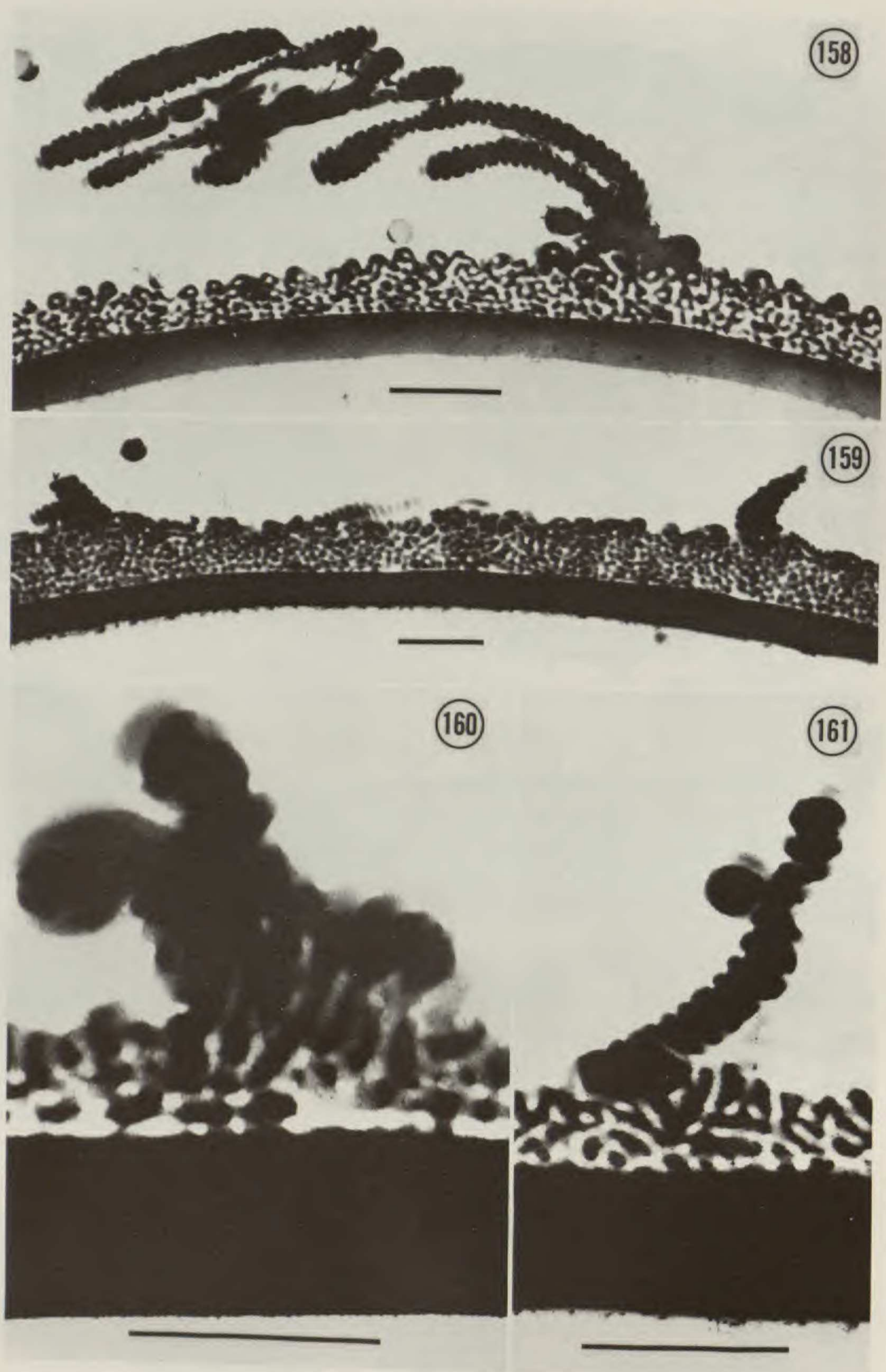
FIGURES 147–150. Scanning (Fig. 147) and transmission (Figs. 148–150) of *Fuchsia* pollen, sect. *Encliandra*, *F. thymifolia* subsp. *minimiflora*. Pollen acetolyzed.—147. The segmented-ropy viscin threads and a coarsely globular surface are similar to *F. thymifolia* subsp. *thymifolia* (Figs. 56, 57).—148. Longitudinal section through segmented thread.—149. Center of the proximal polar face.—150. Same pollen section as Figure 149 but directly opposite distal polar face. The scale equals 1 μm .



FIGURES 151-154. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia*, *F. boliviana*. All pollen rehydrated.—151. Section through middle of distal polar face.—152. Same pollen grain as in Figure 151 but section from center of proximal polar face. In contrast to Figure 151, the ektexine is somewhat thinner.—153. Section at proximal polar face primarily to show relationship of viscin threads to the ektexine, as well as their appearance in different sectional views.—154. Section through a group(s) of viscin threads. The major distinction between acetolyzed and unacetolyzed viscin threads, apart from electron density, is that the latter always appear to be enclosed by a membrane (Figs. 152-154, 157, 164-167, 173, 178, 192) while the former are not (Figs. 117, 127, 158-161, 163, 179). The scale equals 1 μ m.



FIGURES 155-157. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia*, *F. verrucosa*. All pollen rehydrated.—155. Oblique section to include just one apertural protrusion.—156. Section through parts of two pollen grains bound together by pollenkit or some other extra-exinous substance. Note the thicker concentration of granular endexine in the lower exine.—157. Longitudinal section through a smooth viscin thread. The scale equals 1 μm .



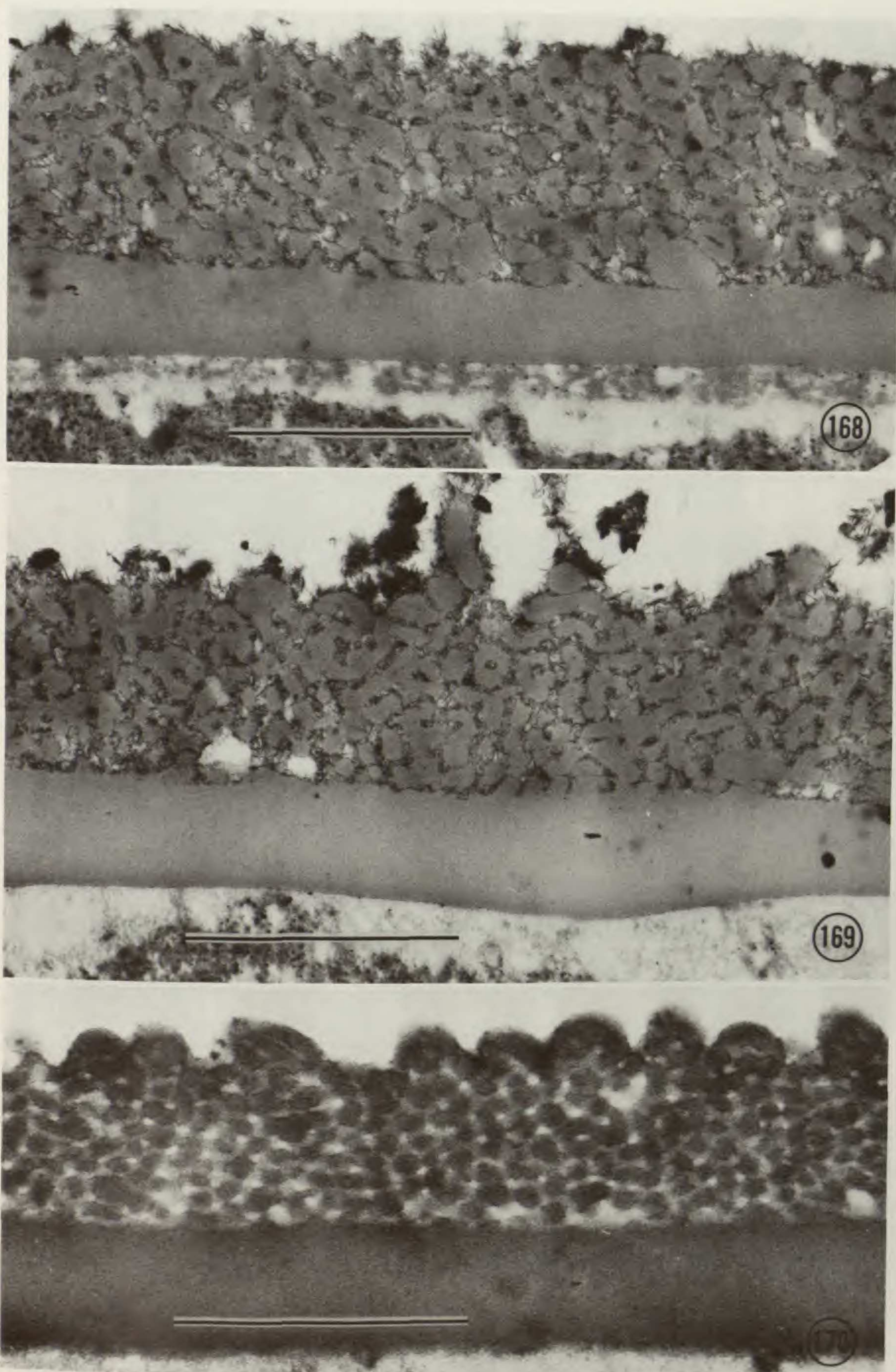
FIGURES 158—161. Transmission electron micrographs of *Fuchsia* pollen, sect. *Fuchsia* (Figs. 158, 159) and sect. *Hemsleyella* (Figs. 160, 161). Pollen acetolyzed. 158, 159. *F. hartwegii*.—158. Section along proximal face surface is somewhat unique in that it includes at least two attachment areas of viscin threads with the ektexine. A thin basal granular endexine component is common. 160, 161. *F. garleppiana*.—160. In this section the ektexine is clearly seen to be an integral part of the viscin threads.—161. Similar to Figure 160. The scale equals 1 μm .



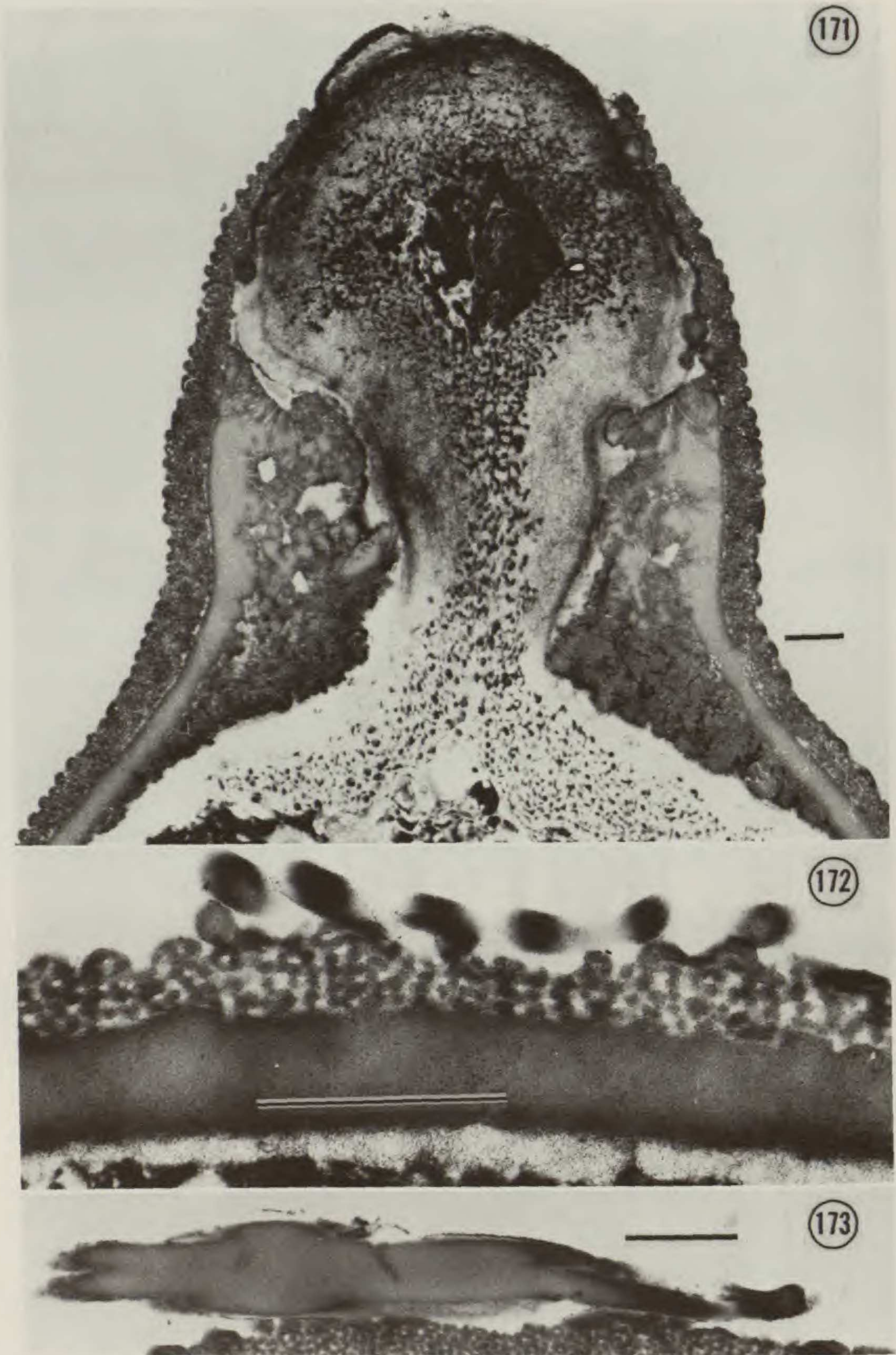
FIGURES 162, 163. Transmission electron micrographs of *Fuchsia* pollen, sect. *Hemsleyella*, *F. garleppiana*. Pollen acetolyzed.—162. High magnification of section through central body.—163. Portion of apertural protrusion. The scale equals 1 μm .



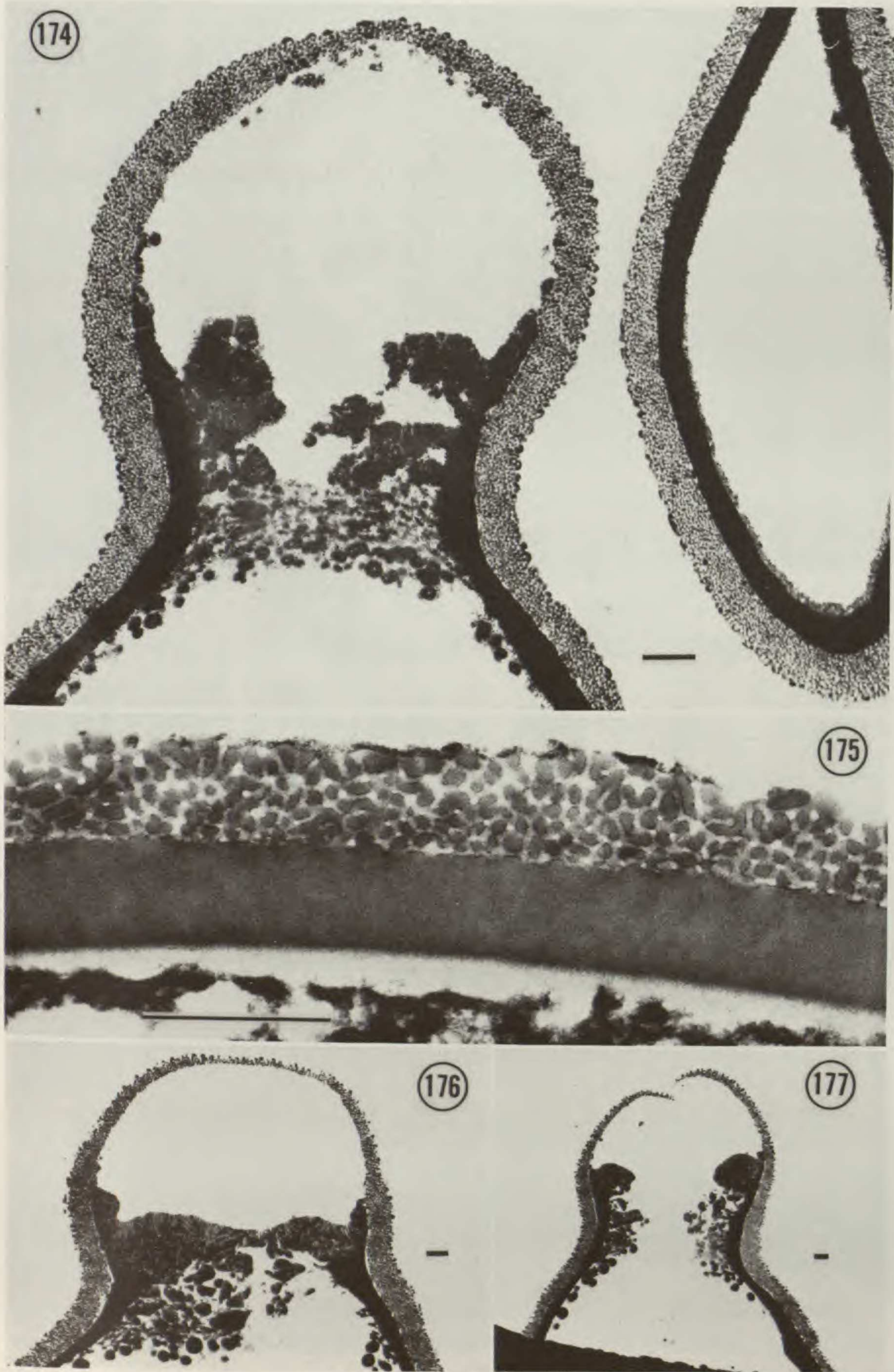
FIGURES 164–167. Transmission electron micrographs of *Fuchsia* pollen, sect. *Hemsleyella*, *F. tillettiana*. All pollen rehydrated.—164. Section at proximal polar surface. Note conspicuous membrane around threads in all figures in this plate.—165. Longitudinal section through four viscin threads.—166. Cross section through a group of viscin threads.—167. Longitudinal section through a single thread clearly showing the segmented-beaded nature. The scale equals 1 μm .



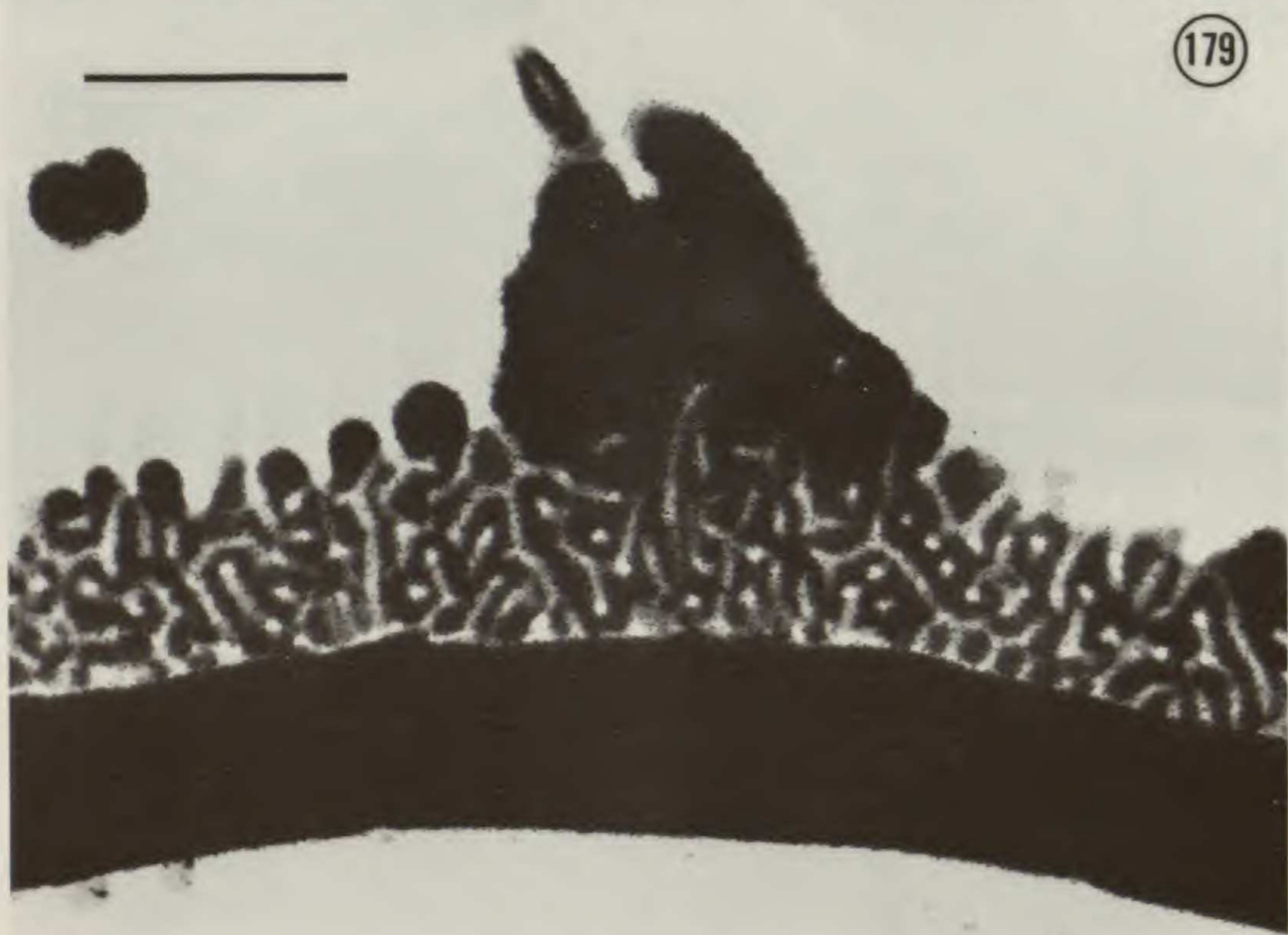
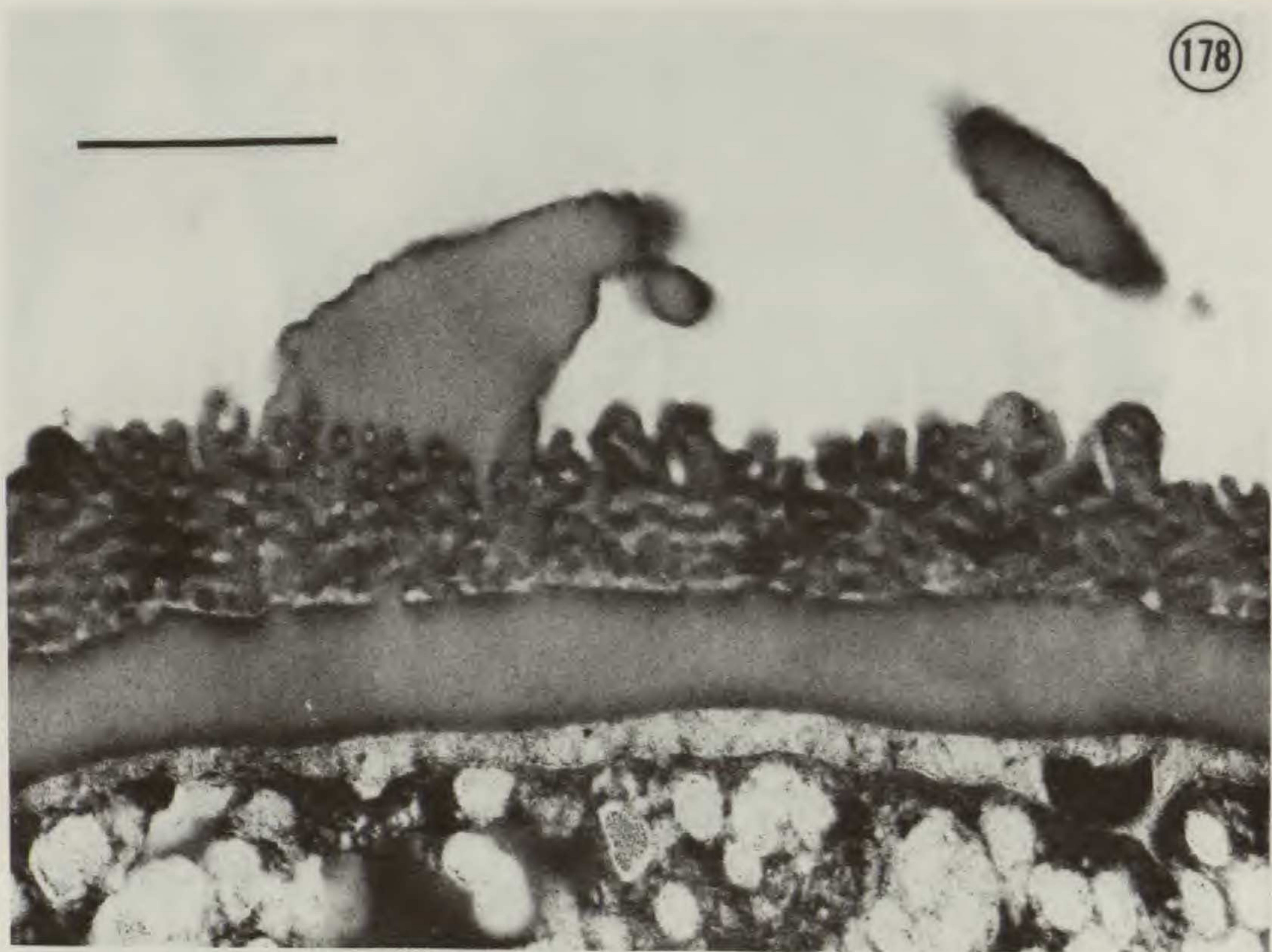
FIGURES 168–170. Transmission electron micrographs of *Fuchsia* pollen, sect. *Jimenezia* (Figs. 168, 169) and sect. *Kierschlegeria* (Fig. 170). All pollen rehydrated. 168, 169. *F. jimenezii*.—168. Section through middle of central body. Note the loosely formed granular endexine. The dense fibrous material on the ectexine surface is a precipitate from staining.—169. Section similar to Figure 115 in that the endexine is tapered at the junction of the apertural protrusion and central body. In this section the granular endexine component is not evident.—170. *F. lycioides*, section at middle of central body. The scale equals 1 μm .



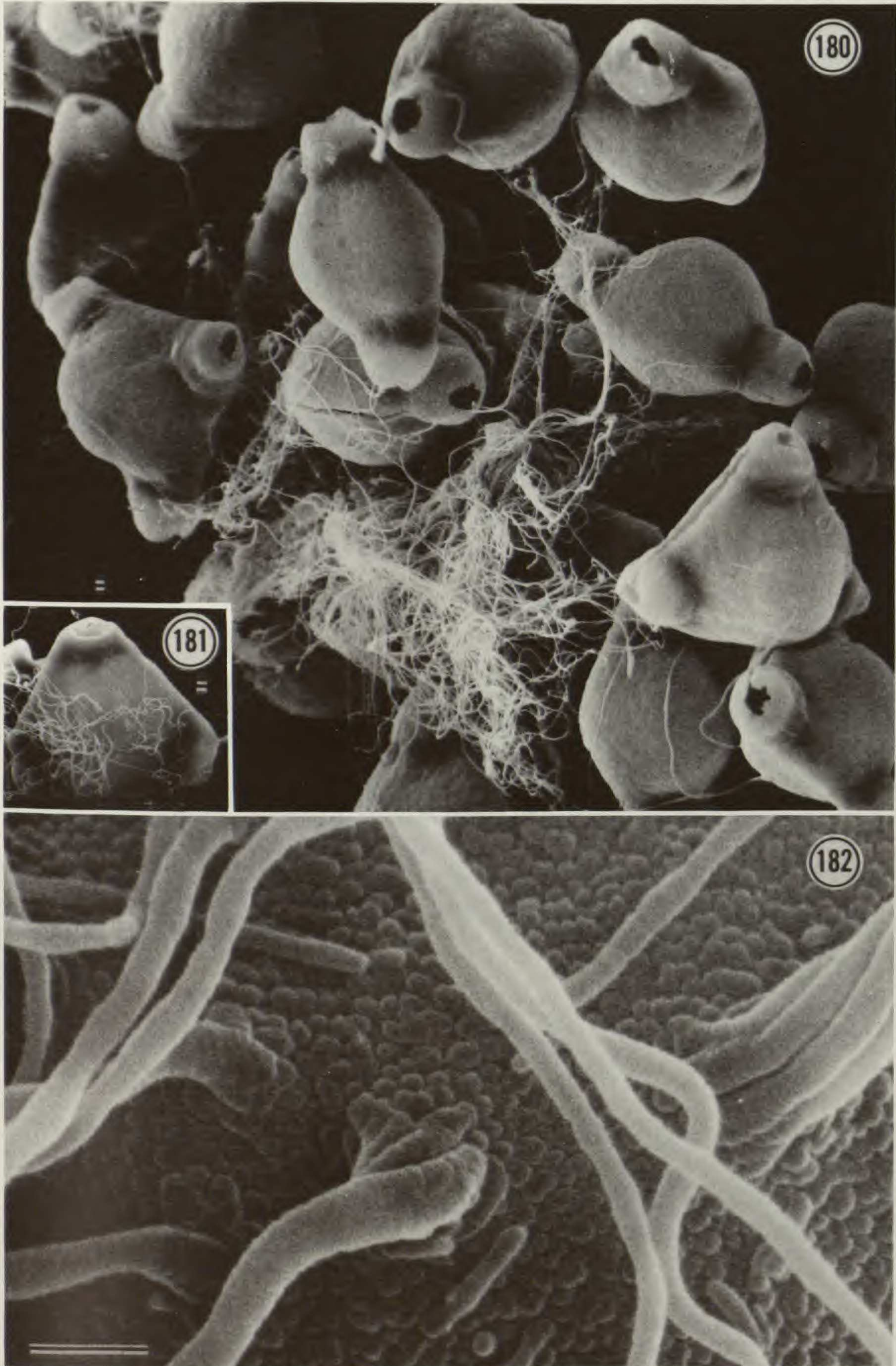
FIGURES 171-173. Transmission electron micrographs of *Fuchsia* pollen, sect. *Kierschlegeria*, *F. lycioides*. All pollen rehydrated.—171. Section through apertural protrusion with cytoplasm extending from the central body (at bottom) through aperture channel and into the vestibulum or aperture chamber.—172. Section at proximal polar surface showing at least six viscin threads in cross sectional view.—173. Longitudinal section of smooth viscin thread group along surface of the ectexine. The scale equals 1 μm .



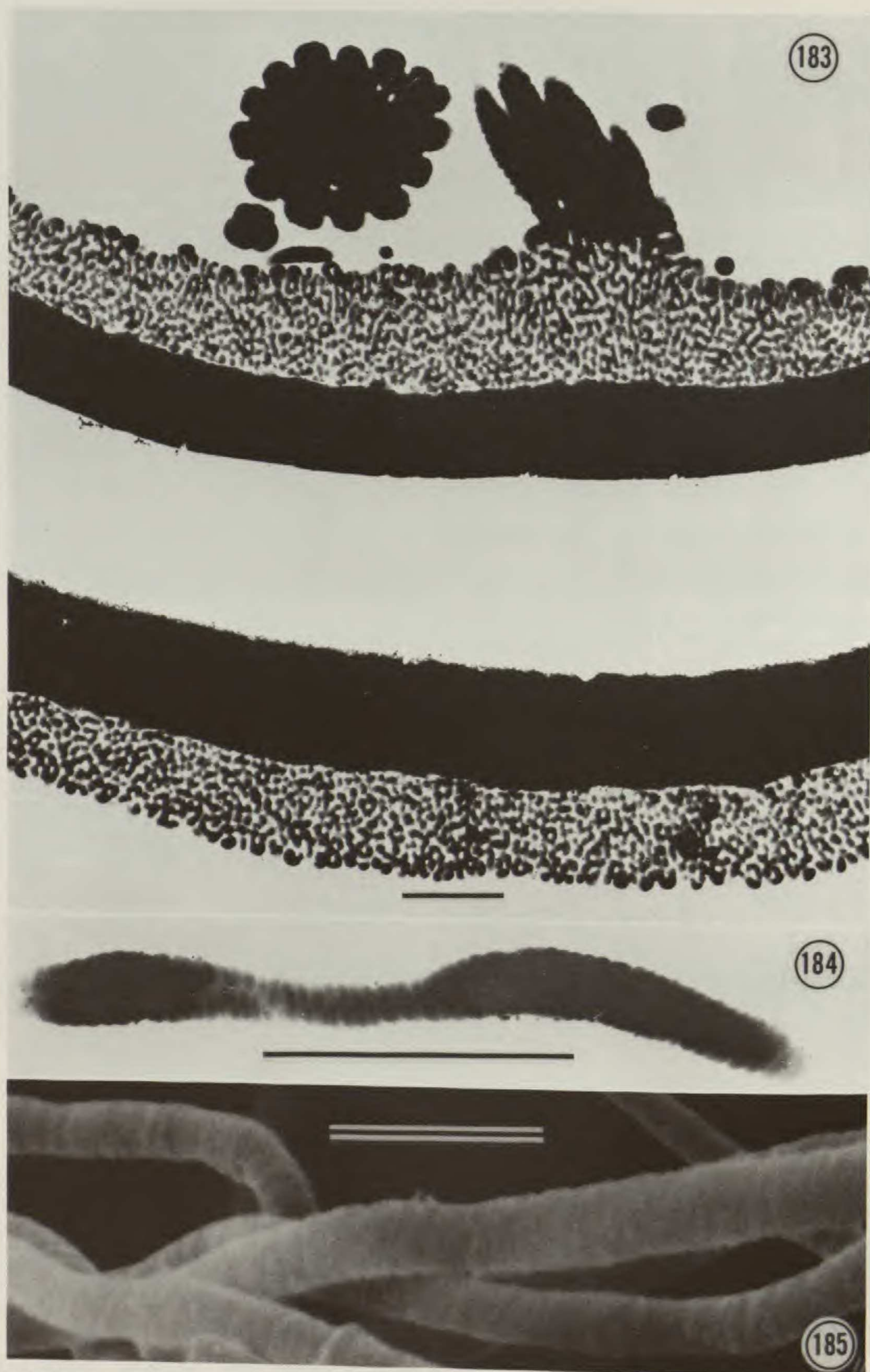
FIGURES 174–177. Transmission electron micrographs of *Fuchsia* pollen, sect. *Quelusia* (Figs. 174, 175) and sect. *Skinnera* (Figs. 176, 177). Acetolyzed (Figs. 174, 176, 177) and rehydrated (Fig. 175) pollen. 174, 175. *F. magellanica*.—174. Section of apertural protrusion (at left) and central body (at right).—175. This rehydrated pollen grain is similar to the acetolyzed grain in Figure 174 except that the ektexine appears to be partially enclosed by a membrane (as noted for the viscin thread) and does not show any granular endexine. 176, 177. *F. excorticata*.—176. This figure and the following (Fig. 177) are sections of the apertural protrusion at different levels. In Figure 176 the honeycombed endexine appears to line the aperture chamber, at least in part.—177. In this figure the section is essentially at mid-level through the center of the apertural protrusion and shows the pore area at the ektexine surface and the apertural channel through the endexine. Note apertural protrusion-central body junction (at right; also see Figs. 115, 169). The scale equals 1 μm .



FIGURES 178, 179. Transmission electron micrographs of *Fuchsia* pollen, sect. *Skinnera*, *F. excorticata*. Rehydrated (Fig. 178) and acetolyzed (Fig. 179) pollen.—178. Section through proximal polar face showing viscin thread attachment with ektexine.—179. Section similar to Figure 178 and included for purpose of comparing acetolyzed and unacetolyzed pollen. The very fine dense granules are probably precipitated from osmic acid stain. The scale equals 1 μ m.



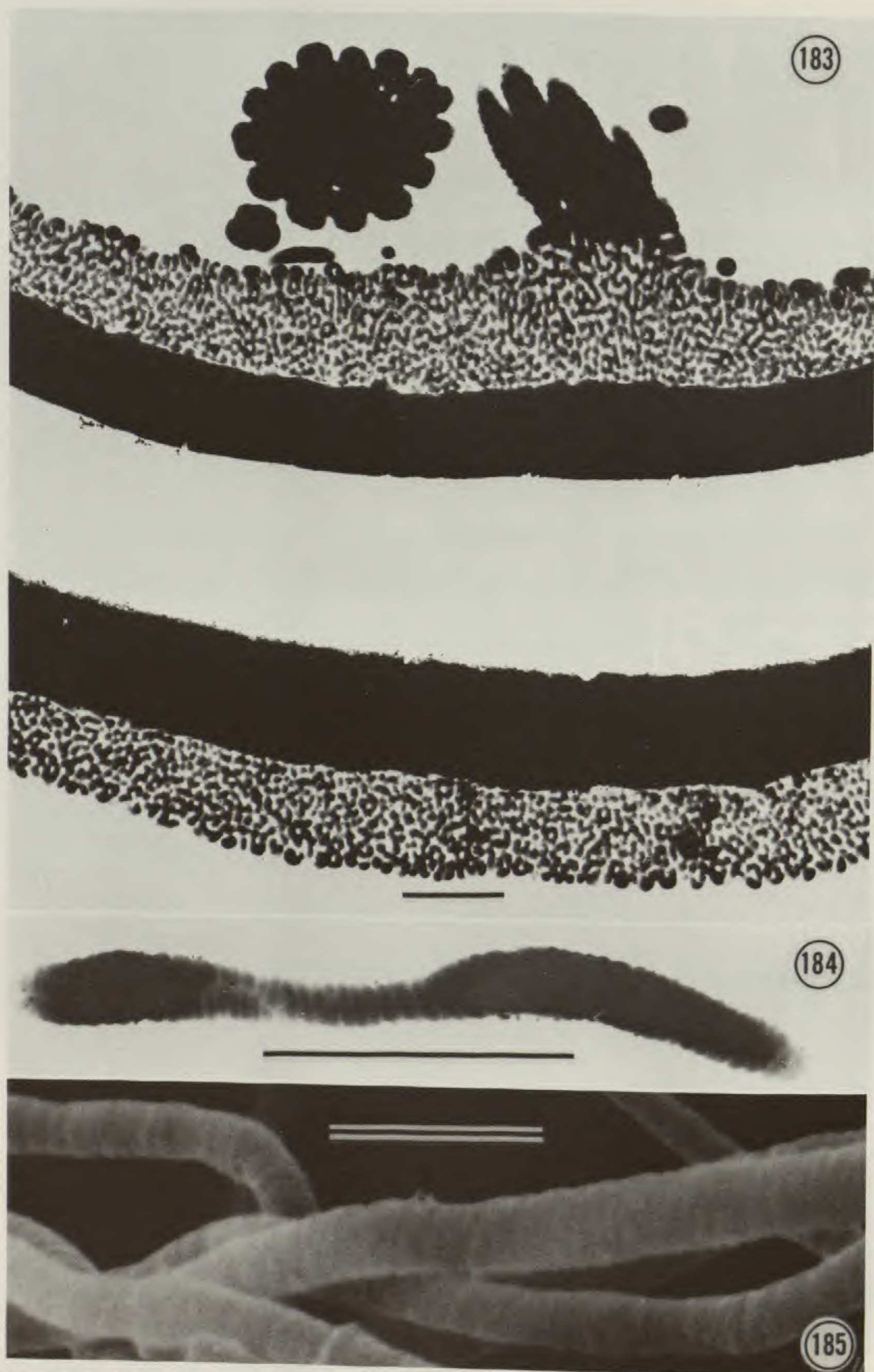
FIGURES 180–182. Scanning electron micrographs of *Fuchsia* pollen, sect. *Skinnera*. Pollen acetolyzed.—180. *F. excorticata*, a few 3-aperturate grains are interspersed with the predominant 2-aperturate grains. 181, 182. *F. cyrtandroides*.—181. A 3-aperturate grain (compare with more common 2-aperturate grains in Figs. 46, 49, 50).—182. Enlargement of proximal surface of Figure 181. Note faint but distinct lightly segmented nature of viscin threads. In Figures 180, 181 the scale equals $2\ \mu\text{m}$; in Figure 182 the scale equals $1\ \mu\text{m}$.



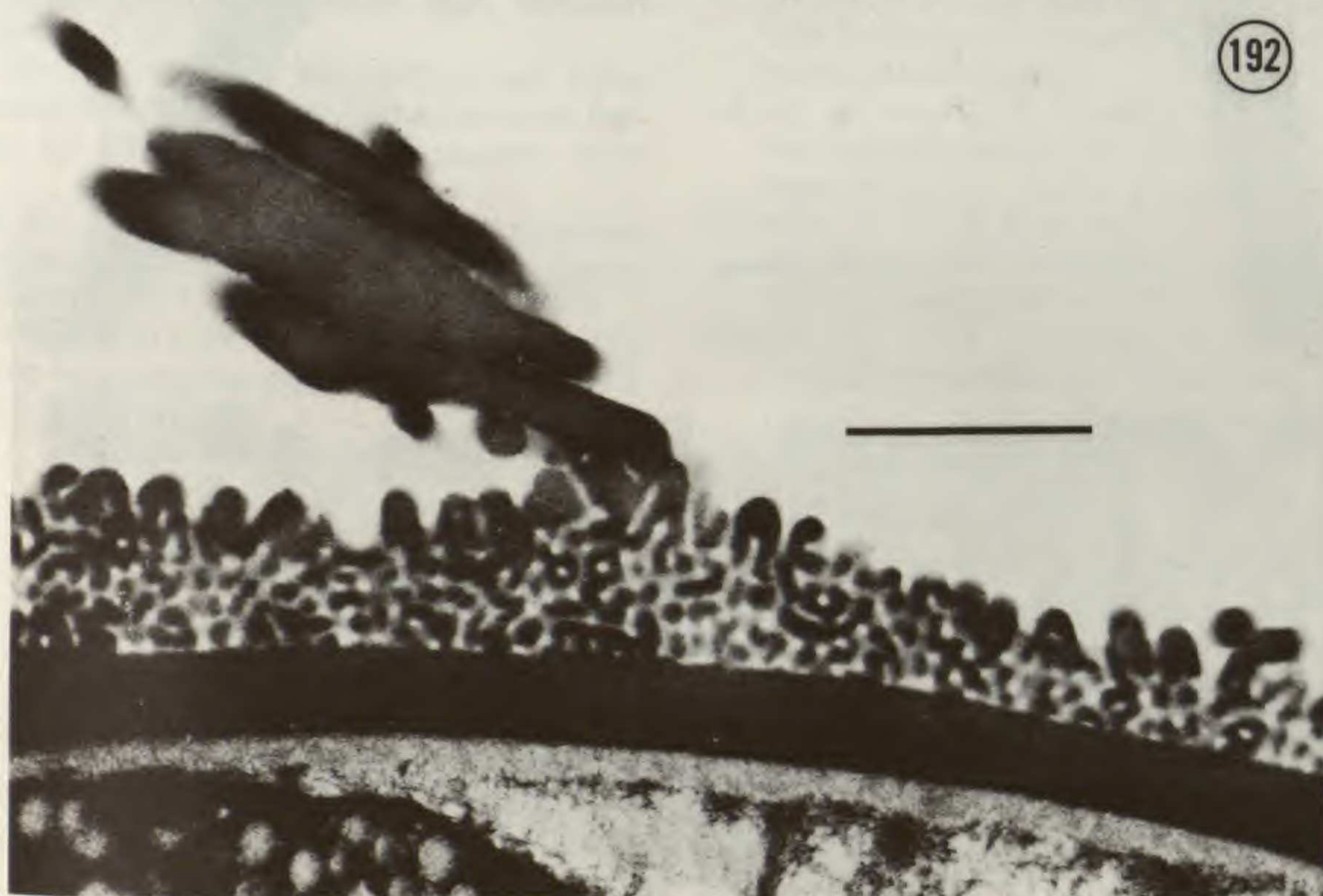
FIGURES 183–185. Scanning (Fig. 183) and transmission (Figs. 184, 185) electron micrographs of *Fuchsia* pollen, sect. *Skinnera*, *F. cyrtandroides*. Pollen acetolyzed.—183. Section includes exine on distal (at bottom) and proximal (at top) polar faces. Note that they are approximately equal. The lightly segmented nature of the viscin threads is evident in some of the threads in the group attached to the ectexine (at right). In the cross section of the thread cluster (at left) the segmented nature of the individual threads is not apparent.—184. Longitudinal section clearly indicating segmented nature of thread.—185. Group of threads from typical 2-aperturate grain showing their lightly segmented nature (compare with Figs. 49, 50, 182). The scale equals 1 μ m.



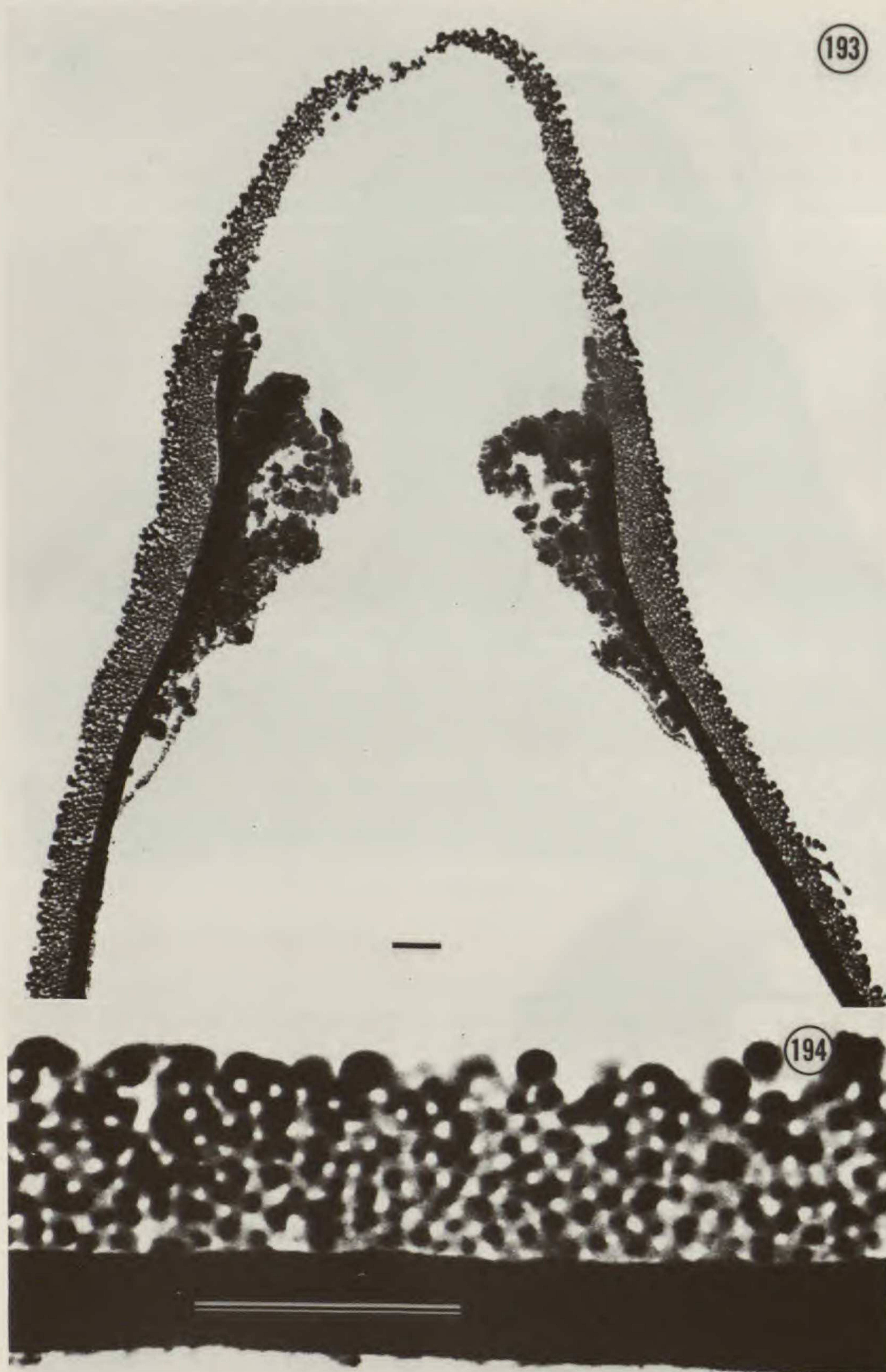
FIGURES 186, 187. Transmission (Fig. 186) and scanning (Fig. 187) electron micrographs of *Fuchsia* pollen, sect. *Skinnera*, *F. perscandens*. Pollen acetolyzed.—186. Section through proximal face. The longitudinal section through the viscin threads indicates their light segmentation (see also Figs. 183, 184).—187. A cluster of threads (approximately equivalent in section view to cross section of thread cluster in Fig. 183). Segmentation of the threads is extremely light. The scale equals 1 μm .



FIGURES 183–185. Scanning (Fig. 183) and transmission (Figs. 184, 185) electron micrographs of *Fuchsia* pollen, sect. *Skinnera*, *F. cyrtandroides*. Pollen acetolyzed.—183. Section includes exine on distal (at bottom) and proximal (at top) polar faces. Note that they are approximately equal. The lightly segmented nature of the viscin threads is evident in some of the threads in the group attached to the ectexine (at right). In the cross section of the thread cluster (at left) the segmented nature of the individual threads is not apparent.—184. Longitudinal section clearly indicating segmented nature of thread.—185. Group of threads from typical 2-aperturate grain showing their lightly segmented nature (compare with Figs. 49, 50, 182). The scale equals 1 μm .



FIGURES 191, 192. Transmission electron micrographs of *Fuchsia* pollen, sect. *Schufia*, *F. arborescens*. All pollen rehydrated.—191. Section through apertural protrusion showing cytoplasm from central body extending through the aperture channel and into the aperture chamber. Note well-defined intine.—192. Section at proximal polar face showing viscin thread attachment with ectexine. The scale equals 1 μm .



FIGURES 193, 194. Transmission electron micrographs of *Fuchsia* pollen, sect. *Schufia*, *F. paniculata*. Pollen acetolyzed.—193. View of apertural protrusion and a portion of the central body.—194. Section through central body. The scale equals 1 μm .

clearly have taxonomic value, aperture number (two versus three) and viscin thread morphology (smooth versus segmented). By using a combination of these features, most sections can be distinguished. Table 2 attempts to correlate these at the sectional level.

LITERATURE CITED

- ATSATT, P. R. & P. RUNDLE. 1982. Pollinator maintenance vs. fruit production: partitioned reproductive effort in subdioecious *Fuchsia lycioides*. *Ann. Missouri Bot. Gard.* 69: 199–208.
- BAKER, H. G. & I. BAKER. 1983. Starchy and starchless pollen in the Onagraceae. *Ann. Missouri Bot. Gard.* 69: 748–754.
- BERRY, P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). *Ann. Missouri Bot. Gard.* 69: 1–198.
- BREEDLOVE, D. E. 1969. The systematics of *Fuchsia* sect. *Encliandra* (Onagraceae). *Univ. Calif. Publ. Bot.* 53: 1–69.
- , P. E. BERRY & P. H. RAVEN. 1982. The Mexican and Central American species of *Fuchsia* (Onagraceae) except sect. *Encliandra*. *Ann. Missouri Bot. Gard.* 69: 209–233.
- CARLQUIST, S. 1975. Wood anatomy of Onagraceae, with notes on alternative modes of photosynthate movement in dicotyledon wood. *Ann. Missouri Bot. Gard.* 62: 386–424.
- ERDTMAN, G. 1966. Pollen Morphology and Plant Taxonomy: Angiosperms (An Introduction to Palynology. I). Hafner Publishing Company, New York.
- EYDE, R. H. & J. T. MORGAN. 1973. Floral structure and evolution in Lopezieae (Onagraceae). *Amer. J. Bot.* 60: 771–787.
- HESSE, M. 1982 [1981]. Pollenkitt and viscin threads: their role in cementing pollen grains. *Grana* 20: 145–152.
- HICKEY, L. J. 1980. Leaf architecture of Onagraceae. P. 69 in Abstracts of the 2nd International Congress of Systematics and Evolutionary Biology, Vancouver, Canada, July 17–24, 1980.
- KURABAYASHI, M., H. LEWIS & P. H. RAVEN. 1962. A comparative study of mitosis in the Onagraceae. *Amer. J. Bot.* 49: 1003–1026.
- MUNZ, P. A. 1943. A revision of the genus *Fuchsia* (Onagraceae). *Proc. Calif. Acad. Sci.* IV 25: 1–138.
- PATEL, V. C., J. J. SKVARLA & P. H. RAVEN. 1984. Pollen characters in relation to the delimitation of Myrtales. *Ann. Missouri Bot. Gard.* 71: (in press).
- POHL, R. W. 1965. Dissecting equipment and materials for the study of minute plant structures. *Rhodora* 67: 95–96.
- PRAGLOWSKI, J., P. H. RAVEN, J. J. SKVARLA & J. W. NOWICKE. 1983. Angiospermae: Onagraceae Juss. Fuchsieae & Jussiaeae. *World Pollen and Spore Flora* 12: 1–41.
- RAVEN, P. H. 1979. A survey of reproductive biology in Onagraceae. *New Zealand J. Bot.* 17: 575–593.
- & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.
- ROWLEY, J. R. & S. NILSSON. 1972. Structural stabilization for electron microscopy of pollen from herbarium specimens. *Grana* 12: 23–30.
- SKVARLA, J. J., P. H. RAVEN & J. PRAGLOWSKI. 1976. Ultrastructural survey of Onagraceae pollen. Pp. 447–479 in I. K. Ferguson & J. Muller (editors), *The Evolutionary Significance of the Exine*. Academic Press, London.
- , ———, W. F. CHISSOE & M. SHARP. 1978. An ultrastructural study of viscin threads in Onagraceae pollen. *Pollen & Spores* 20: 5–143.
- SUSSMAN, R. W. & P. H. RAVEN. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. *Science* 200: 731–736.
- WARTH, G. 1925. Zytologische, histologische und stammesgeschichtliche Fragen aus der Gattung *Fuchsia*. *Z. Indukt. Abstammungs-Vererbungs.* 28: 200–257.